MycoKeys

MycoKeys 120: 193–229 (2025)
DOI: 10.3897/mycokeys.120.153906

Research Article

Additions of New Endolichenic Fungi to Herpotrichiellaceae (Chaetothyriales, Ascomycota) from northern Thailand

Chanokned Senwanna[1,2], Jaturong Kumla[1,2,3], Pratthana Kodchasee[2], Nutchanan Duangkon[2], Nakarin Suwannarach[1,2,3]

1 *Office of Research Administration, Chiang Mai University, Chiang Mai 50200, Thailand*
2 *Center of Excellence in Microbial Diversity and Sustainable Utilization, Chiang Mai University, Chiang Mai 50200, Thailand*
3 *Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand*

Corresponding author: Nakarin Suwannarach (suwan.462@gmail.com)

Abstract

Endolichenic fungi associated with lichen thalli in Thailand are poorly known in terms of species diversity. During a study conducted in Chiang Mai Province, Thailand, in 2023, eight endolichenic fungal strains were isolated from healthy thalli of the foliose lichen, *Parmotrema* sp. These eight strains were identified as members of the family Herpotrichiellaceae using a combination of three nuclear ribosomal regions (ITS, LSU, and SSU), *tub2* sequence data, and morphological characteristics. Two strains of *Atrokylindriopsis racemosospora* and three strains of *Veronaea endolichena* were identified as new species within the Herpotrichiellaceae, while three other strains were identified as the previously known species *Phialophora chinensis*. This study provides the first report of *P. chinensis* as an endolichenic fungal taxon and its first discovery in Thailand. Descriptions, illustrations, and phylogenetic placements of these eight strains are provided. Additionally, a discussion and update on the ecology and genera within the Herpotrichiellaceae are included. The findings of this study offer valuable information that enriches the diversity of endolichenic species associated with lichens in Thailand and contributes to enhancing our understanding of the ecology and taxonomy of the Herpotrichiellaceae.

Key words: Chaetothyriales, endolichenic fungi, fungal diversity, fungal taxonomy, lichen, new taxa

OPEN ACCESS

Academic editor: Gerhard Rambold
Received: 25 March 2025
Accepted: 10 July 2025
Published: 30 July 2025

Citation: Senwanna C, Kumla J, Kodchasee P, Duangkon N, Suwannarach N (2025) Additions of New Endolichenic Fungi to Herpotrichiellaceae (Chaetothyriales, Ascomycota) from northern Thailand. MycoKeys 120: 193–229. https://doi.org/10.3897/mycokeys.120.153906

Copyright: © Chanokned Senwanna et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

The family Herpotrichiellaceae (Chaetothyriales, Eurotiomycetes) was established by Munk (1953) and typified by *Herpotrichiella moravica*, which is synonymized under *Capronia pilosella* based on the teleomorph-anamorph connection (Müller et al. 1987; Untereiner 1997). The sexual morph of Herpotrichiellaceae is characterized by setose, ostiolate ascomata, bitunicate, saccate to ovoid asci with a thickened apex and long endotunica, and didymosporous, phragmosporous, or dictyosporous ascospores. The asexual morph consists of morphologically diverse dematiaceous hyphomycetes, predominantly characterized by black yeast (Müller et al. 1987; Untereiner et al. 1995; Arzanlou et al. 2007; Tian et al. 2021). These fungi primarily reproduce asexu-

ally, and exhibit limited morphological characters (Untereiner et al. 1995; Moreno et al. 2018; Tian et al. 2021). The internal transcribed spacer (ITS) and the large subunit (LSU) of ribosomal DNA sequences are commonly used to clarify the taxonomic placement of members in the Herpotrichiellaceae; however, many genera in this family have shown polyphyletic relationships (Quan et al. 2020; Tian et al. 2021; Torres-Garcia et al. 2023). Multi-gene sequence data are essential for resolving the morphological confusion among these genera and for establishing boundaries between genera and species. Species of Herpotrichiellaceae are not only recognized for causing human infections but also for their extremotolerance, thriving in a wide range of environments worldwide, including extreme conditions of high or low temperature, nutrient scarcity, desiccation, and solar irradiation (Müller et al. 1987; Untereiner 1997; Arzanlou et al. 2007; Teixeira et al. 2017; Muggia and Grube 2018; Quan et al. 2020, 2024; Chang et al. 2023; Thitla et al. 2023; Torres-Garcia et al. 2023; Diederich et al. 2024). Before this study, nineteen genera were recognized in this family, *viz*. *Aciculomyces*, *Aculeata*, *Atrokylindriopsis*, *Capronia*, *Cladophialophora*, *Exophiala*, *Fonsecaea*, *Marinophialophora*, *Melanoctona*, *Minimelanolocus*, *Petriomyces*, *Phialophora*, *Phaeoannellomyces*, *Pleomelogramma*, *Rhinocladiella*, *Thysanorea*, *Uncispora*, *Valentiella*, and *Veronaea* (Tian et al. 2021; Bezerra et al. 2022; Thitla et al. 2023; Torres-Garcia et al. 2023).

Lichens are ubiquitous on a wide range of surfaces and can occur in various environmental conditions (Müller 2001; Molnár and Farkas 2010; Lücking et al. 2017; Muggia and Grube 2018). They serve not only as bioindicators for assessing air pollution and evaluating environmental health, but also serve as sources of secondary metabolites with diverse pharmaceutical properties (Casale et al. 2015; Crawford 2019; Panta 2020; Wethalawe et al. 2021; Zhao et al. 2021). Lichen thalli provide a habitat conducive to the growth of other photosynthetic and non-photosynthetic organisms, such as algae, bacteria, filamentous fungi, and yeast, while shielding the photobiont from external harm (Suryanarayanan and Thirunavukkarasu 2017; Hawksworth and Grube 2020). Many lichen-associated fungi, including both endolichenic and lichenicolous fungi, are currently being studied and described at both morphological and molecular levels (Wang et al. 2016; Cometto et al. 2023, 2024; Si et al. 2023). Lichenicolous fungi are visible inhabitants of lichen thalli, whether they are host-specific parasites, saprotrophs, broad-spectrum pathogens, or commensals (Lawrey and Diederich 2003; Diederich et al. 2018). In contrast, endolichenic fungi are non-obligate fungi that colonize the internal tissues of lichen thalli without causing visible symptoms or negative effects. Their occurrence is similar to that of endophytic fungi (Arnold et al. 2009; Gao et al. 2016; Kellogg and Raja 2017; Elkhateeb and Daba 2021). Since lichenicolous fungi have been shown to be present in asymptomatic lichens, differentiating between lichenicolous and endolichenic fungi can be scientifically challenging (Yang et al. 2022). Species diversity of endolichenic fungi influenced not only by lichen host species but also by the environment, habitat, host, and geographic distribution (U'Ren et al. 2012; Gao et al. 2016; Muggia and Grube 2018; Agrawal et al. 2020; Elkhateeb and Daba 2021). Moreover, studies on the diversity of endolichenic fungi in recent years have relied on culture-based and metabarcoding approaches (U'Ren et al. 2010; Zhang et al. 2016; Fernández-Mendoza et al. 2017; Yang et al. 2021; Si et al. 2023). According to several previous studies, ascomycetes are the dominant group

of endolichenic fungi associated with lichens, followed by basidiomycetes and mucoromycetes. (Gao et al. 2016; Muggia and Grube 2018; Chakarwarti et al. 2020; Elkhateeb and Daba 2021; Cometto et al. 2024). Concurrently, various endolichenic fungal genera associated with lichen thalli worldwide have been identified, including *Aspergillus*, *Chaetomium*, *Cladophialophora*, *Cladosporium*, *Penicillium*, *Rhinocladiella*, *Trichoderma*, and *Xylaria* (Muggia et al. 2017; Maduranga et al. 2018; Muggia and Grube 2018; Yang et al. 2021; Cometto et al. 2023, 2024). Thailand has a humid tropical climate and is recognized as one of the most biodiverse countries in the world (Tungmunnithum et al. 2022; Kaewsangsai et al. 2024). Numerous studies have been conducted on bacteria, insects, plants, fungi (endophytes, saprophytes, and pathogens), and lichens; however, the diversity of endolichenic fungi remains relatively unexplored (Tanasupawat 2009; Maneechan and Prommi 2015; Dathong 2016; Buaruang et al. 2017; Hyde et al. 2018; Jayawardena et al. 2020; Tayung 2022; Bamrungpanichtavorn et al. 2023; Krongdang et al. 2023; Kaewsangsai et al. 2024; Nimnoi et al. 2024). Therefore, this research aimed to study the diversity of endolichenic fungi in Thailand. During a 2023 study of endolichenic fungi in northern Thailand, eight fungal strains belonging to the family Herpotrichiellaceae were isolated from foliose lichen thalli (*Parmotrema* sp.), including three strains of *Phialophora chinensis* and five strains of unidentified fungal taxa. Based on morphology, growth temperature, and multi-gene phylogenetic analyses, five Herpotrichiellaceous fungi are identified as novel taxa. Additionally, we provide an update on the ecology and genera within the Herpotrichiellaceae family.

Materials and methods

Lichen collection

The foliose lichen thalli of *Parmotrema* sp. were collected from Chai Prakan and Mueang Chiang Mai Districts, Chiang Mai Province, northern Thailand, during June to July 2023. During the collection period, Chai Prakan District experienced daily rainfall of 81.2 mm, with a temperature range of 27 °C to 36 °C, whereas Mueang Chiang Mai District received daily rainfall of 153.2 mm, with temperatures ranging from 24 °C to 34 °C. Healthy specimens were carefully removed from tree bark using a sterile knife, transferred into individual plastic bags, the collection details were recorded (Rathnayaka et al. 2024), and the specimens were stored at 4 °C until processing within 48–96 hours after sampling.

Fungal isolation

The lichen thalli were carefully observed under an Olympus SZ40 stereo microscope to avoid damage and prevent contamination of any parts. Fungal isolation was performed following the protocols of Maduranga et al. (2018) and Si et al. (2023), with some modifications. The healthy lichen thalli were thoroughly washed in running water for 10 min to remove excess dirt and dried with sterile paper towels. The thalli were randomly dissected aseptically into 1 cm^2 fragments using a sterile razor blade under a stereo microscope, followed by surface sterilization with immersion in 70% ethanol for 1 min, 1% NaOCl for 1 min, and rinsing three times in sterile distilled water for 1 min. The upper and lower

cortex layers of surface-sterilized lichen fragments were carefully scratched under a stereo microscope using a sterile surgical blade and tweezers. The medulla tissue was carefully removed and cleaned with sterile distilled water. The fragment was then cut into a 0.5 cm^2 segment. Six lichen segments were evenly placed in a 9 cm Petri dish containing potato dextrose agar (PDA; Condalab, Laboratorios Conda S.A., Spain) and dichloran rose-bengal agar (DRBC; Difco, Becton, Dickinson and Company, USA). For each specimen, three replications of the isolation plates were made. The plates were incubated at 25 °C until the growth of endolichenic fungi. The fungal hypha that grew from the segments was transferred onto freshly prepared PDA plates and incubated at 25 °C. The pure fungal strains were stored short-term on PDA slants at 4 °C and long-term in 20% glycerol at −80 °C at the Sustainable Development of Biological Resources culture collection (SDBR-CMU), Faculty of Science, Chiang Mai University, located in Chiang Mai Province, Thailand. Additionally, fungal strains were deposited and permanently maintained in a metabolically inactive state at the Chiang Mai University Biology Department's Herbarium (CMUB), Chiang Mai University, Chiang Mai Province, Thailand. New fungal taxa were registered in the MycoBank database (MycoBank 2025).

Morphological studies

Pure fungal colonies were investigated on different media for induce pigmentation and sporulation viz., corn meal agar (CMA; Difco, BBL™, USA), cornmeal dextrose agar (CMD; Difco corn meal agar + 2% dextrose), malt extract agar (MEA; Gibco, Life Technologies Corporation, USA), oatmeal agar (OA; Difco, Becton, Dickinson and Company, USA) and potato carrot agar (PCA; 200 g of each boiled and filtered carrots and potatoes, 17 g agar, 1 L distilled water). Mycelial plugs (3 mm × 3 mm) from 7-day-old PDA culture were cultured on each medium. The plates were incubated at 25 °C. In addition, the cardinal growth temperatures at 4, 25, 30, and 35 °C of fungal strains were determined on MEA for two weeks in the dark. Microscopic features, including mycelia, branching patterns, and sporulating structures, were observed and photographed using a Nikon DS-Ri2 camera connected to a Nikon ECLIPSE Ni (Tokyo, Japan) compound microscope. The fungal structure measurement was performed using the Tarosoft Image Framework program (v. 0.9.0.7). Adobe Photoshop version 22.4.2 (Adobe Systems U.S.A.) was employed to create the photographic plates.

DNA extractions, polymerase chain reaction, and sequencing

DNA extractions were performed using the Fungal DNA Extraction Kit (FAVORGEN, Ping-Tung, Taiwan) from mycelium scraped from colonies grown on PDA using a sterile scalpel. DNA concentration and quality were determined by NanoDrop One^C Microvolume UV-Vis Spectrophotometer (Thermo Scientific, Wilmington, DE, USA). The nuclear ribosomal internal transcribed spacer (ITS) region, 28S large subunit (LSU), 18S small subunit (SSU), and beta tubulin gene (*tub2*) were amplified using ITS4/ITS5 (White et al. 1990), LR0R/LR5 (Vilgalys and Hester 1990), NS1/NS4 (White et al. 1990), and Bt2a/Bt2b (Glass and Donaldson 1995) primers, respectively. Polymerase chain reaction (PCR) amplification was

performed using peqSTAR thermal cycler (PEQLAB Ltd., Fareham, UK) in a final volume of 20 µL containing 10 µL of 2 × Quick TaqTM HS DyeMix (TOYOBO, Japan), 6 µL of sterile deionized water, 1 µL of 10 µM of each forward and reverse primer, and 2 µL of DNA. The PCR conditions for ITS, LSU, and SSU amplification were as follows: initial denaturing step of 95 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 45 s, elongation at 72 °C for 1 min, and final extension at 72 °C for 10 min. The PCR conditions for *tub2* amplification were as follows: initial denaturing step of 94 °C for 4 min, followed by 35 cycles of denaturation at 94 °C for 40 s, annealing at 52 °C for 30 s, elongation at 72 °C for 1 min, and final extension at 72 °C for 7 min. The PCR product was checked by 1% agarose electrophoresis gels under UV light. PCR clean-up Gel extraction NucleoSpin® Gel and PCR Clean-up Kit (Macherey-Nagel, Germany) was used to purify the PCR products according to the manufacturer's protocol, which were sequenced by 1st BASE Company (Kembangan, Malaysia). New sequences generated in this study were deposited in GenBank.

Sequence alignment and phylogenetic analyses

The ITS, LSU, SSU, and *tub2* sequence data were edited, quality-checked, and assembled using the SeqMan 5.00 software. The consensus sequences were BLAST-searched using the NCBI nucleotide database (http://blast.ncbi.nlm.nih.gov/) to assess the closely related species. Sequences generated in the analyses were chosen from related sequences of the genera in Herpotrichiellaceae which were derived from GenBank and recent publications (Su et al. 2023; Thitla et al. 2023; Torres-Garcia et al. 2023). *Cyphellophora laciniata* (CBS 190.61) and *C. suttonii* (CBS 449.91) were selected as the out-group taxa (Table 1).

The alignment of each locus was conducted using the MAFFT sequence alignment server (Katoh et al. 2019; http://mafft.cbrc.jp/alignment/server/) and improved manually where necessary in BioEdit v.7.0.9.1 (Hall 1999). Sequence data for ITS and LSU were analyzed individually to examine the incongruence in the topology of the phylogenetic tree. Concatenated ITS, LSU, SSU, and *tub2* sequence data were then analyzed and used to generate phylogenetic trees based on maximum likelihood (ML) and Bayesian inference (BI) methods.

The ML tree was executed using the GTRGAMMA substitution model of nucleotide substitution and set to 1,000 bootstrapping replicates via the CIPRES web portal. The BI tree was executed using a Markov Chain Monte Carlo (MCMC) algorithm with MrBayes v. 3.2.6 (Ronquist et al. 2012), employing the best-fit model of sequence evolution determined by MrModeltest v. 2.3 (Nylander 2008). The GTR+I+G substitution model was the best-fitting model of sequence evolution, which was determined based on the Akaike Information Criterion (AIC) using the MrModeltest v2.3 (Nylander 2008) implemented in PAUP v. 4.0b10 (Swofford 2002). Parameters for Bayesian inference: Four simultaneous Markov chains were set to run 20,000,000 generations, with the tree sampling every 100th generation, resulting in 200,000 trees. The first 25% of generated trees as part of a burn-in procedure were discarded, and the remaining trees were evaluated for posterior probabilities (PP) of a majority rule consensus tree. The resulting trees from ML and BI were displayed using FigTree v1.4.0 (Rambaut 2016) and modified using Adobe Illustrator Version 25.2.3 and Adobe Photoshop Version 22.4.2 (Adobe Systems, United States of America).

Table 1. Taxa used in this study, along with their corresponding GenBank accession numbers. Ex-type strains are indicated with superscript "T". The taxa obtained in this study are in bold. "–" is indicated the absence of sequence data in GenBank.

Taxa name	Strain number	GenBank Accession number			
		ITS	LSU	SSU	*tub2*
Aciculomyces restrictus	FMR 18994^{T}	ON009870	ON009950	–	ON667802
Aculeata aquatica	MFLUCC 11-0529^{T}	MG922571	MG922575	MG922579	–
Atrokylindriopsis setulosa	HMAS245592^{T}	KP337330	KP337329	–	–
Atrokylindriopsis racemosospora	**SDBR-CMU502^{T}**	**PQ525388**	**PQ525396**	**PQ525404**	**PQ523731**
Atrokylindriopsis racemosospora	**SDBR-CMU503**	**PQ525389**	**PQ525397**	**PQ525405**	**–**
Capronia acutiseta	CBS 618.96^{T}	AF050241	KF155191	AJ232942	–
Capronia camelliae-yunnanensis	CGMCC 3.19061^{T}	MH807377	MH807378	MH807379	–
Capronia dactylotricha	CBS 604.96^{T}	AF050243	KX712343	AJ232943	–
Capronia leucadendri	CBS 122672^{T}	EU552108	MH874754	–	–
Capronia nigerrima	CBS 513.69	MH859363	AY605075	AY541478	–
Capronia pilosella	AFTOL-ID 657^{T}	DQ826737	DQ823099	DQ823106	–
Cladophialophora abundans	CBS 126736^{T}	KC776592	KC812100	–	–
Cladophialophora arxii	CBS 306.94^{T}	EU103986	KX822320	–	–
Cladophialophora bantiana	CBS 173.52^{T}	EU103989	KF155189	–	–
Cladophialophora carrionii	CBS 160.54^{T}	EU137266	FJ358234	FJ358302	EU137201
Cladophialophora denticulata	FMR 18992^{T}	ON009845	ON009925	–	ON667783
Cladophialophora devriesii	CBS 147.84^{T}	EU103985	KC809989	AJ232947	–
Cladophialophora emmonsii	CBS 979.96^{T}	EU103996	–	–	–
Cladophialophora exuberans	CMRP1227^{T}	KY680429	KY570931	–	KY689826
Cladophialophora heterospora	FMR 18641^{T}	ON009847	ON009927	–	ON491592
Cladophialophora immunda	CBS 834.96^{T}	MH862619	KC809990	KF155194	EU137203
Cladophialophora inabaensis	EUCL1^{T}	LC128795	–	–	–
Cladophialophora lanosa	KNU 16032^{T}	LC387460	LC387461	–	–
Cladophialophora mycetomatis	CBS 122637^{T}	FJ385276	KX822321	KX822278	–
Cladophialophora nyingchiensis	CGMCC 3.17330^{T}	MG012699	MG197824	MG012728	MG012747
Cladophialophora psammophila	CBS 110553^{T}	AY857517	KX712346	–	–
Cladophialophora recurvata	CBS 143843^{T}	LT985878	LT985879	–	LT985894
Cladophialophora rupestricola	SDBR-CMU446^{T}	OP903465	OP903502	OR141860	OR139230
Cladophialophora samoensis	CBS 259.83^{T}	MH861581	KC809992	KX822281	EU137174
Cladophialophora sribuabanensis	SDBR-CMU476^{T}	OQ991178	OQ979608	OR141868	OR139238
Cladophialophora subtilis	CBS 122642^{T}	FJ385273	KX822322	KX822283	–
Cladophialophora tengchongensis	CGMCC3.15201^{T}	MG012702	MG197827	MG012731	MG012750
Cladophialophora thailandensis	SDBR-CMU451^{T}	OP903470	OP903507	OR141865	OR139235
Cladophialophora tumulicola	JCM 28766^{T}	LC192098	LC192063	–	–
Cladophialophora yegresii	CBS 114405^{T}	EU137322	KC809994	KX822284	EU137209
Cyphellophora laciniata	CBS 190.61^{T}	EU035416	FJ358239	FJ358307	JQ766329
Cyphellophora suttonii	CBS 449.91^{T}	KC455243	KC455256	KC455300	KC455226
Exophiala bonariae	CBS 139957^{T}	JX681046	KR781083	–	–
Exophiala brunnea	CBS 587.66^{T}	MH858890	KX712342	JN856013	JN112442
Exophiala candelabrata	FMR 18336^{T}	ON009851	ON009931	–	ON491591
Exophiala opportunisticica	CBS 109811^{T}	KF928437	KF928501	–	JN112486
Exophiala palmae	UPCB 86822^{T}	KY680434	KY570929	–	KY689829
Exophiala pisciphila	CBS 537.73^{T}	DQ826739	AF050272	DQ823108	JN112493
Exophiala radicis	P2854^{T}	KT099204	KT723448	KT723453	KT723463
Exophiala salmonis	CBS 157.67^{T}	JF747137	AY213702	EF413608	JN112499
Exophiala siamensis	SDBR-CMU417^{T}	ON555811	–	ON555826	ON544240
Exophiala siamensis	SDBR-CMU418	ON555812	–	ON555827	ON544241
Fonsecaea brasilliensis	CBS 119710^{T}	JN173784	KF155183	KF155203	JN368478
Fonsecaea erecta	CBS 125763^{T}	KC886414	KF155186	KF155210	KF155221
Fonsecaea monophora	CBS 102243^{T}	EU938579	FJ358247	FJ358315	EU938542
Fonsecaea multimorphosa	CBS 980.96^{T}	JF267657	KF155188	JF433950	HQ681121
Fonsecaea pedrosoi	CBS 271.37^{T}	AB114127	KJ930166	AY554290	EU938559
Marinophialophora garethjonesii	MFLUCC 16-1449	KY305174	KY305177	KY305178	–
Marinophialophora garethjonesii	KUMCC 16-0066^{T}	KY305175	KY305176	KY305179	–
Melanoctona tectonae	MFLUCC 12-0389^{T}	KX258778	KX258779	KX258780	–
Petriomyces obovoidisporus	SDBR-CMU478^{T}	OQ991180	OQ979610	OR141870	OR139240
Petriomyces obovoidisporus	SDBR-CMU479	OQ991181	OQ979611	OR141871	OR139241

Taxa name	Strain number	GenBank Accession number			
		ITS	LSU	SSU	*tub2*
Phaeoannellomyces elegans	CBS 122.95^{T}	KY115190	–	–	–
Phaeoannellomyces elegans	CBS 101597	KF928443	KF928507	–	KF928571
Phialophora americana	CBS 281.35	EU514694	EU514694	–	EU514707
Phialophora americana	CBS 400.67	EU514695	EU514695	–	EU514708
Phialophora americana	UAMH 10875^{T}	EU514696	EU514696	–	EU514712
Phialophora americana	UAMH 10876	EU514697	EU514697	–	EU514713
Phialophora chinensis	BMU 02669	KF881930	KJ930045	–	KF971731
Phialophora chinensis	CBS 140326^{T}	KF881964	KJ930093	KM658060	KF971765
Phialophora chinensis	IFM 51934	AB550779	AB550779	–	–
Phialophora chinensis	BMU 00447	KF881957	KJ930082	–	KF971757
Phialophora chinensis	BMU 00150	KJ700947	KJ930077	–	KM658123
Phialophora chinensis	BMU 01057	KJ700953	KJ930086	–	KM658129
Phialophora chinensis	BMU 07661	KJ701013	KJ930155	–	KM658101
Phialophora chinensis	BMU 07656	KJ700998	KJ930152	–	KM658107
Phialophora chinensis	BMU 07664	KJ701003	KJ930156	–	KM658111
Phialophora chinensis	**SDBR-CMU504**	**PQ525390**	**PQ525398**	**PQ525406**	**PQ523732**
Phialophora chinensis	**SDBR-CMU505**	**PQ525391**	**PQ525399**	**PQ525407**	**PQ523733**
Phialophora chinensis	**SDBR-CMU506**	**PQ525392**	**PQ525400**	**PQ525408**	**PQ523734**
Phialophora ellipsoidea	CBS 286.47^{T}	AF050282	AF050282	–	EU514715
Phialophora ellipsoidea	CBS 224.97	U31848	–	–	KU306354
Phialophora expanda	BMU 01245	KF881934	KJ930088	–	KF971734
Phialophora expanda	CBS 140298^{T}	KF881937	KJ930095	–	KF971737
Phialophora macrospora	CBS 273.37^{T}	AF050281	AF050281	–	EU514714
Phialophora macrospora	CBS 138.67	KU306356	–	–	KU306355
Phialophora tarda	CBS 111589^{T}	KU306362	–	–	KU306347
Phialophora submersa	FMR 17150^{T}	ON009864	ON009944	–	ON667800
Phialophora submersa	FMR 18996	ON009867	ON009947	–	ON667798
Phialophora submersa	FMR 18997	ON009868	ON009948	–	ON667799
Phialophora verrucosa	CBS 140325^{T}	NR146242	KJ930073	NG061187	KF971761
Rhinocladiella anceps	CBS 181.65^{T}	EU041805	EU041862	AY554292	–
Rhinocladiella atrovirens	CBS 317.33^{T}	AB091215	MH866906	–	–
Rhinocladiella mackenziei	CBS 650.93^{T}	AY857540	AF050288	–	–
Rhinocladiella phaeophora	CBS 496.78^{T}	EU041811	EU041868	EF137366	GU079661
Rhinocladiella quercus	CBS 141448^{T}	KX306769	KX306794	–	–
Thysanorea aquaticus	MFLUCC 15-0414	KR215607	KR215612	KR215617	–
Thysanorea clavatus	DLU 3022^{T}	MT271774	MT271772	MT271777	–
Thysanorea papuana	CBS 212.96^{T}	MH862572	MH874198	–	–
Thysanorea submersus	KUMCC 15-0206^{T}	KX789212	KX789215	–	–
Thysanorea thailandensis	MFLUCC 15-0971^{T}	MG922573	MG922577	MG922581	–
Uncispora sinensis	YMF 1.03683^{T}	KU173860	KU558914	KU558913	–
Uncispora wuzhishanensis	YMF 1.04080^{T}	KU173859	KU558912	KU558911	–
Valentiella maceioensis	BSS 376	MZ042488	MZ042486	–	–
Valentiella maceioensis	CBS 141892^{T}	KY305141	KX348014	–	–
Veronaea aquatica	JAUCC2549^{T}	MW046892	MW046893	–	MW248394
Veronaea botryosa	CBS 254.57^{T}	MH857711	MH869255	JN856021	JN112505
Veronaea botryosa	MFLUCC 11-0072	MG922570	MG922574	MG922578	–
Veronaea botryosa	CBS 102593	KF928429	KF928493	–	KF928557
Veronaea botryosa	CBS 572.90	MH862237	MH873920	–	–
Veronaea botryosa	GZCC 19-0557	OP377853	OP377938	OP378020	–
Veronaea compacta	CBS 268.75^{T}	EU041819	EU041876	–	–
Veronaea endolichena	**SDBR-CMU507^{T}**	**PQ525393**	**PQ525401**	**PQ525409**	**PQ523735**
Veronaea endolichena	**SDBR-CMU508**	**PQ525394**	**PQ525402**	**PQ525410**	**PQ523736**
Veronaea endolichena	**SDBR-CMU509**	**PQ525395**	**PQ525403**	**PQ525411**	**PQ523737**
Veronaea japonica	CBS 776.83^{T}	EU041818	EU041875	–	–
Veronaea polyconidia	CGMCC 3.25589^{T}	OR807862	OR807868	OR807865	OR817660
Veronaea polyconidia	UESTCC 23.0138	OR807863	OR807869	OR807866	OR817661
Veronaea polyconidia	UESTCC 23.0139	OR807861	OR807867	OR807864	OR817659

Results

Phylogenetic analyses

The concatenated ITS, LSU, SSU, and *tub2* sequence dataset consists of 114 representative strains of species in the families Herpotrichiellaceae and Cyphellophoraceae (outgroup). The total alignment length comprises 3,413 characters (ITS: 1–779; LSU: 780–1,644; SSU: 1,645–2,872; *tub2*: 2,873–3,413), including gaps. The topologies of the trees generated from ML and BI analyses were congruent. The resultant ML tree is shown in Fig. 1. The best RAxML tree with a final likelihood optimization value of -32004.987525 is presented. The matrix contained 1,459 distinct alignment patterns, with 38.84% of the characters being undetermined or gaps. Estimated base frequencies were as follows: A = 0.251383, C = 0.234823, G = 0.265952, T = 0.247842; substitution rates AC = 1.510868, AG = 3.198001, AT = 1.566806, CG = 0.906099, CT = 6.013302, GT = 1.000000; gamma distribution shape parameter α = 0.548282. The average standard deviation of split frequencies was 0.009767 at the end of total MCMC generations.

The phylogenetic tree, based on the analysis of a combined ITS, LSU, SSU, and *tub2* sequence data, shows the relationships of taxa within the family Herpotrichiellaceae (Fig. 1). The results indicated that all eight endolichenic fungal strains obtained in this study belong to the family Herpotrichiellaceae. Three strains (SDBR-CMU504, SDBR-CMU505, and SDBR-CMU506) clustered within the *Phialophora* species and were found to be phylogenetically related to *P. chinensis*, with 86% ML and 1 PP statistical support. Interestingly, the other five strains formed distinct lineages from previously known taxa. Two fungal strains (SDBR-CMU502 and SDBR-CMU503) of a novel taxon formed a monophyletic clade clustering with *Atrokylindriopsis setulosa*, with 100% ML and 1 PP support values. In addition, three remaining strains (SDBR-CMU507, SDBR-CMU508, and SDBR-CMU509) are also introduced as a new species, which forms a distinct lineage in *Veronaea* with 92% ML and 1 PP and is in a sister clade to *V. botryosa*.

Taxonomic descriptions

Atrokylindriopsis racemosospora **Senwanna, J. Kumla & N. Suwannar., sp. nov.**
MycoBank No: 858499
Fig. 2

Etymology. In reference to the spore arrangement resembling a raceme form.

Type. THAILAND • Chiang Mai Province: Chai Prakan District, Nong Bua Subdistrict, endolichenic from the medulla of foliose lichen (*Parmotrema* sp.) on *Prunus domestica*, 19°42'23"N, 99°1'32"E, elevation 1160 m, 2 June 2023, C. Senwanna and N. Suwannarach, CMUB40067 (***Holotype***, preserved in a metabolically inactive state. ***Ex-type*** living culture LC05-1 = SDBR-CMU502).

Cultural characteristics. Colonies on different agar media were incubated in the dark at 25 °C for 2 months; colonies flat, irregular, with edge undulate, velvety; on PDA (18 to 27 mm in diameter) surface grayish brown, light brown at the margin, reverse olivaceous black, light brown at the margin; on MEA (18 to 23 mm in diameter) surface grayish brown, dark brown to black at the margin, reverse olivaceous black, producing brown pigment in agar;

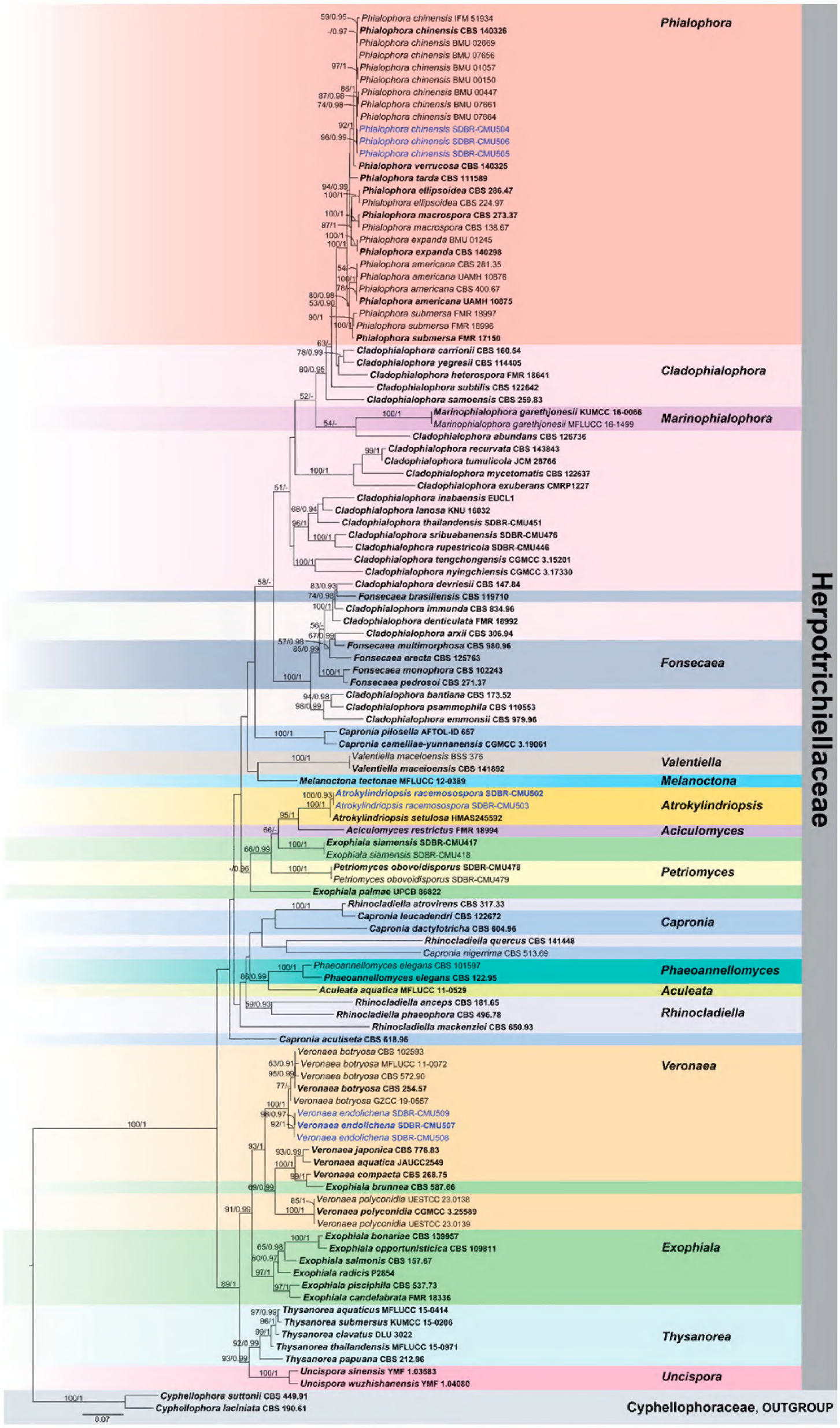

Figure 1. Phylogram generated from maximum likelihood analysis of members in Herpotrichiellaceae based on a combined ITS, LSU, SSU, and *tub2* sequence dataset. Bootstrap values ≥ 50% MLBS and Bayesian posterior probabilities (PP) ≥ 0.90 are shown above nodes and defined as ML/PP. The tree is rooted to *Cyphellophora laciniata* (CBS 190.61) and *C. suttonii* (CBS 449.91). The fungal strains obtained in this study are blue. Ex-type strains are in bold. The scale bar represents the expected number of nucleotide substitutions per site.

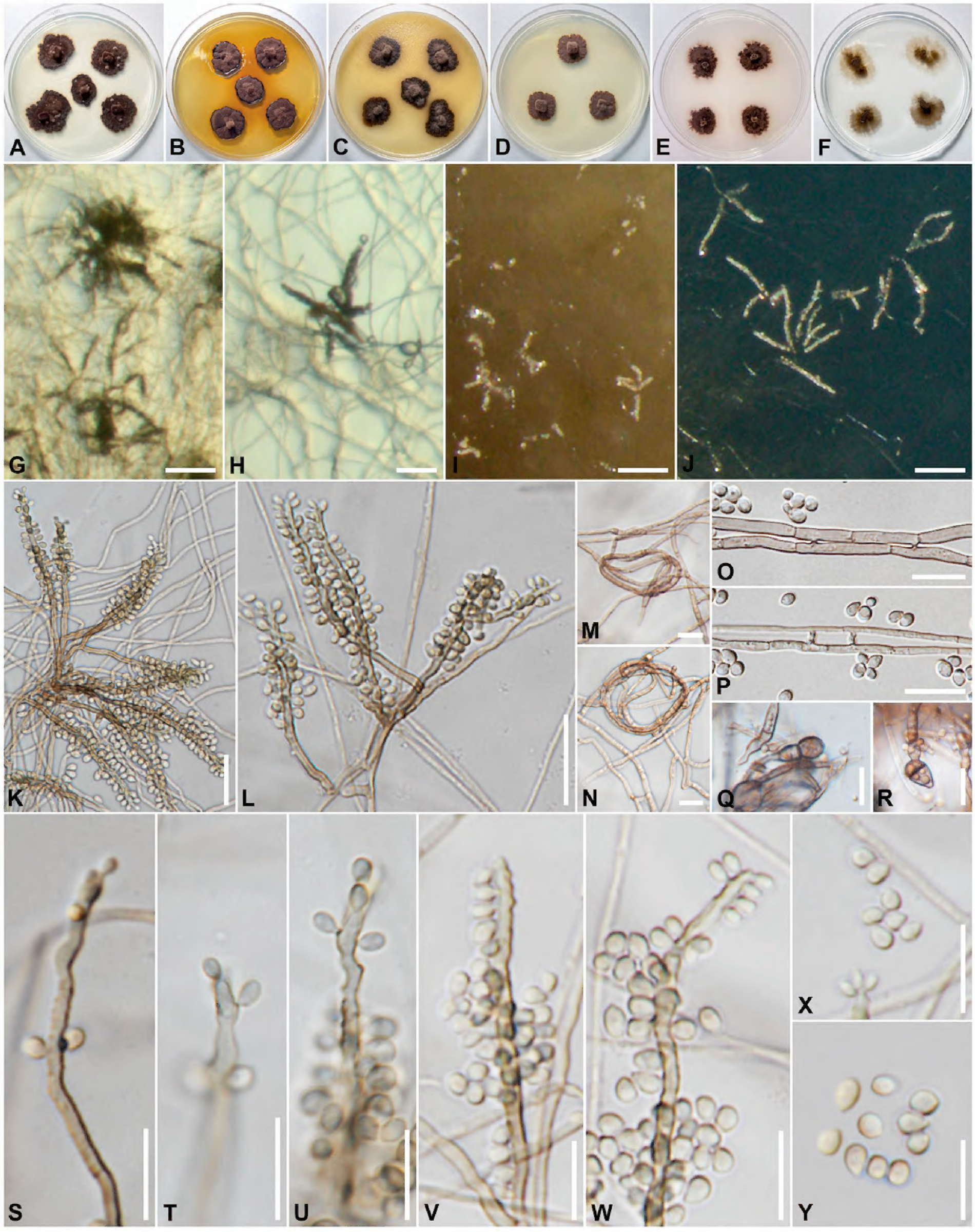

Figure 2. *Atrokylindriopsis racemosospora* (SDBR-CMU502, ex-type). **A–F.** Colonies on PDA, MEA, OA, PCA, CMD and CMA, respectively, after 48 d at 25 °C; **G, H.** Conidiophores sporulating on PCA; **I.** Conidiophores sporulating on OA; **J.** Conidiophores sporulating on CMA; **K, L.** Conidiophores and conidia; **M–N.** Hyphal coil; **O, P.** Hyphal anastomosis; **Q, R.** Terminal chlamydospores; **S–W.** Conidiophores with conidiogenous loci; **X–Y.** conidia. Scale bars: 10 µm (**G–J**); 20 µm (**K–L**); 10 µm (**M–Y**).

on OA (17 to 23 mm in diameter) surface grayish brown, reverse olivaceous black, sporulation absent; on PCA (17 to 20 mm in diameter) surface and reverse brownish gray, reverse olivaceous black, sporulation absent. On CMD (15 to 20 mm in diameter) surface and reverse grayish brown; and on CMA (20 to 27 mm in diameter) surface and reverse brownish grey, sporulation absent. ***Asexual morph in vitro*** dematiaceous hyphomycetes. ***Hyphae*** 1–2.5 µm wide, pale brown, simple to branched, septate, smooth, thin-walled, coiling, anastomosis observed. ***Conidiophores*** (10–)20–111(–153) × (1.4–)1.8–2.6(–2.9) µm ($\overline{x}$ = 53.17 × 2.15, *n* = 40), macronematous, monomematous, straight or slightly flexuous, unbranched, continuous or 1–3 septate, dark brown, paler terminally, smooth-, thick-walled. ***Conidiogenous cells*** (6.6–)15.5–36(–45.5) × (1.4–)1.8–2.6(–2.9) µm ($\overline{x}$ = 25.5 × 2.16, *n* = 40), integrated, polyblastic, terminal to mostly intercalary, proliferating sympodial and producing conidia from short denticles, subcylindrical, pale brown to brown, fertile parts subhyaline; denticles scattered, slightly darkened, 0.4–1 µm wide. ***Conidia*** (2.5–)2.8–4.4(–5) × (1.8–)2–3.3 µm ($\overline{x}$ = 3.72 × 2.68, *n* = 40), abundant, obovoid or subglobose, with a round apex, and slightly truncate base, aseptate, subhyaline to pale brown, smooth-walled, with inconspicuous conidial scars, 0.5–1 µm wide. ***Chlamydospores*** rare, solitary or in chains, terminal, globose to pyriform, without or one-septate, pigmented, dark brown, smooth-, thick- walled. ***Sexual morph*** unknown.

Cardinal temperatures for growth on MEA after two weeks (mm). Optimum at the range of 25 °C to 30 °C (10 to 14). No growth 4 °C and 35 °C.

Additional materials examined. Thailand • Chiang Mai Province, Chai Prakan District, Nong Bua Subdistrict, endolichenic from the medulla of foliose lichen (*Parmotrema* sp.) on *Prunus domestica*, 19°42'23"N, 99°1'32"E, elevation 1160 m, 2 June 2023, C. Senwanna and N. Suwannarach, living culture (LC05-3 = SDBR-CMU503).

Additional GenBank numbers. *act* and *tef1* for SDBR-CMU502: PQ523738 and PQ523739; *tef1* for SDBR-CMU503: PQ523740.

Ecology and distribution. Endolichenic fungi from the medulla of foliose lichen (*Parmotrema* sp.) in Thailand.

Notes. Based on a blast search of the NCBI's GenBank nucleotide database of the ITS sequence, *Atrokylindriopsis racemosospora* has the closest match with *At. setulosa* (strain HMAS245592; KP337330, ex-type) with 99.33% similarity and is similar to *Aciculomyces restrictus* (strain FMR 18994; ON009870, ex-type) with 93.79% similarity (identities = 468/499, 10 gaps) and *Exophiala siamensis* (strain SDBR-CMU417; NR_184988, ex-type) with 92.39% similarity (identities = 583/631, 16 gaps). The closest matches using the LSU sequence are *At. setulosa* (strain HMAS245592; KP337329) with 100% similarity (identities = 548/548, 0 gap), *Ex. ramosa* (strain FMR 18632; ON009933, ex-type) with 98.97% similarity (identities = 865/874, 1 gap), and *Melanoctona tectonae* (strain MFLUCC 12-0389; NG_059687) with 98.43% similarity (identities = 879/893, 2 gaps). The closest matches using SSU sequence are *Ex. siamensis* (strain SDBR-CMU417; ON555826) with 99.53% similarity (identities = 1055/1060, 1 gap), *Capronia dactylotricha* (strain CBS 604.96; NG_062636) with 98.45% similarity (identities = 1082/1099, 1 gap), and *E. yunnanensis* (strain YMF1.06739, ex-type) with 98.31% similarity (identities = 1049/1067, 1 gap). The closest matches

using the *tub2* sequence are *Biscogniauxia arima* (strain YMJ 122; AY951672) with 93.08% similarity (identities = 121/130, 1 gap) and *B. mediterranea* (strain ISN9LDC31; OQ942633) with 92.37% similarity (identities = 121/131, 1 gap).

A combined multilocus-based phylogenetic analysis showed that both strains (SDBR-CMU502 and SDBR-CMU503) of *Atrokylindriopsis racemosospora* formed sister taxon to *At. setulosa* (HMAS245592, ex-type strain) with 100% ML and 1 PP statistical support, and also clustered with *Aciculomyces restrictus* (FMR 18994, ex-type strain) with 95% ML and 1 PP statistical support (Fig. 1). The ITS and LSU nucleotide sequence comparisons reveal 3/580 and 0/548 base pair differences with *At. setulosa*, respectively. In contrast, a comparison of ITS, LSU, *tef1*, and *tub2* base pairs shows that *At. racemosospora* differs from *Ac. restrictus* by 34/494 bp of ITS, 8/770 bp of LSU, 38/158 bp of *tef1*, and 108/430 bp of *tub2*. The morphology of *Atrokylindriopsis* differs from that of *Aciculomyces* in having unbranched, macronematous conidiophores, monophialidic conidiogenous cells, pigmented, septate, setulate conidia (Ma et al. 2015; Torres-Garcia et al. 2023). *Atrokylindriopsis racemosospora* shares similar features, including sympodial proliferation, denticulate conidiogenous cells, and aseptate, obovoid or subglobose conidia, with species *Ac. restrictus* (Torres-Garcia et al. 2023), but *Ac. restrictus* has longer conidiophores (10–153 × 1.4–2.9 µm *vs* 19–105.5 × 1.5–2.5 µm) and smaller conidia (2.5–5 × 1.8–3.3 µm *vs* 2–4 × 1.5–2.5 µm). Moreover, the conidiogenous cells and conidia formation of *At. racemosospora* is more abundant than that of *Ac. restrictus*, and the conidial scars are not conspicuous. In addition, *At. setulosa* differs from *At. racemosospora* by its larger, cylindrical to clavate or rounded-cuboid conidia, which have 4–5 longitudinal eusepta and are attached to the conidiogenous locus at the midpoint of their long side, appearing to form a 'T' (Ma et al. 2015). These morphological characteristics clearly distinguish *At. racemosospora* from *Ac. restrictus* and *At. setulosus*.

Phialophora chinensis **Ya L. Li, de Hoog & R.Y. Li, in Li, Xiao, de Hoog Wang, Wan, Yu, Liu & Li, Persoonia 38: 11 (2016)**

MycoBank No: 815345

Fig. 3

Cultural characteristics. Colonies on different agar media were incubated in the dark at 25 °C for 1 months; colonies flat, irregular, with edge entire, velvety; on PDA (39 to 44 mm in diameter) surface grayish brown, dark brown to black at the margin, reverse olivaceous black; on MEA surface Blackish Grey, black at the margin, reverse olivaceous black; on MEA (49 to 53 mm in diameter) surface Blackish Grey, black at the margin, reverse olivaceous black; on OA (69 to 74 mm in diameter) surface grayish brown, reverse olivaceous black; on PCA (46 to 55 mm in diameter) surface and reverse grayish brown, dark brown at the margin, reverse olivaceous black, sporulation absent; on CMD (42 to 50 mm in diameter) surface and reverse brownish gray; and on CMA (33 to 41 mm in diameter) surface and reverse brownish grey, sporulation absent. ***Asexual morph in vitro*** dematiaceous hyphomycetes. ***Hyphae*** 1–3.4 µm wide, subhyaline to light brown, simple to branched, septate, smooth-, thin-walled, coiling, anastomosis observed. ***Conidiophores*** (4–)5.5–31(–45.3)

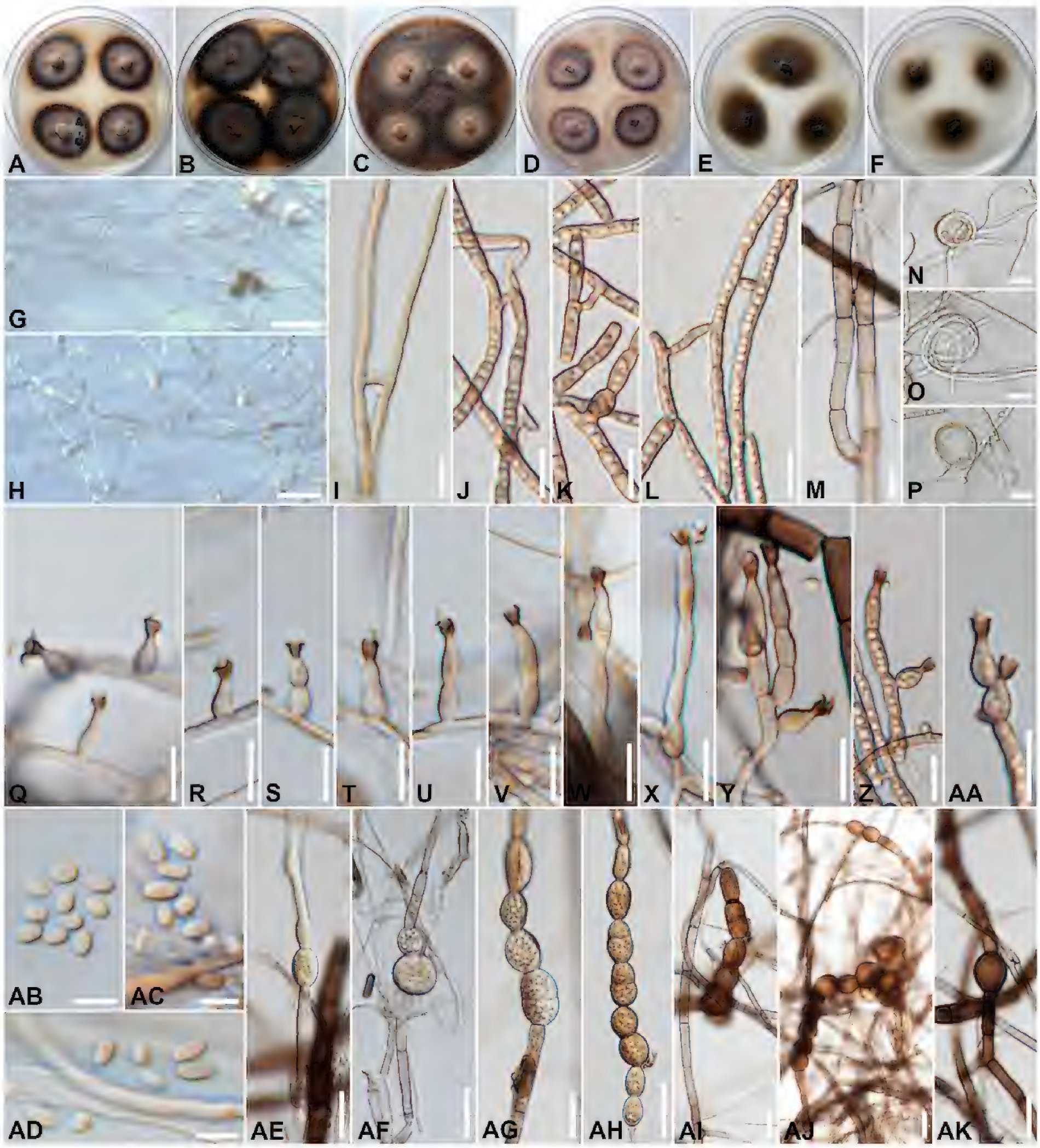

Figure 3. *Phialophora chinensis* (SDBR-CMU506, new host record). **A–F.** Colonies on PDA, MEA, OA, PCA, CMD and CMA, respectively, after 30 d at 25 °C; **G.** Conidiophores sporulating on CMA; **H.** Conidiophores sporulating on PCA; **I–M.** Hyphal anastomosis; **N–P.** Hyphal coil; **Q–AA.** Phialides at different stages of development; **AB–AD.** Conidia; **AE–AK.** Chlamydospores (intercalary and chains formation). Scale bars: 100 µm (**G, H**); 10 µm (**I–AA**); 5 µm (**AB–AD**); 20 µm (**AE–AK**).

× (2–)3–4.3(–4.8) µm ($\bar{x}$ = 17 × 3.6, *n* = 55), micro- or semi-macronematous, straight, simples or poorly branched, septate, slightly constricted at septa, smooth; micronematous conidiophores consisting in conidiogenous cells growing directly from vegetative hyphae, lateral or terminal. ***Phialides*** 4–11(–15.5) × 2.3–4(–5) µm ($\bar{x}$ = 8.3 × 3.3, *n* = 75), regularly flask-shaped to elongate-ampulliform or subulate, with an apical conspicuous collarette; collarettes (1.6–)2–3.9(–4.8) × (1.6–)2–3.9(–4.2) µm ($\bar{x}$ = 3 × 3, *n* = 65),

usually funnel-shaped, darker than the rest of the phialide. ***Conidia*** 2–4(–5) × 1.6–2.7(–3.9) µm ($\bar{x}$ = 3.3 × 2.2, *n* = 75), hyaline to subhyaline, mostly broadly ellipsoidal, more rarely obovoidal, smooth-walled. ***Chlamydospores*** 9.5–20(–23) µm wide, abundantly produced in aerial hyphae, mostly intercalary, solitary or in branched chains, sub globose to ellipsoidal or barrel-shaped, pigmented, light to dark brown, smooth-, thick-, dark-walled, without or one-septate, constricted near the septa. ***Sexual morph*** unknown.

Cardinal temperatures for growth on MEA after two weeks (mm). Optimum at the range of 25 °C to 30 °C (19 to 24), maximum 35 °C (17 to 19). No growth 4 °C.

Materials examined. THAILAND • Chiang Mai Province: Mueang Chiang Mai District, Suthep Subdistrict, endolichenic from the medulla of foliose lichen (*Parmotrema* sp.) on unidentified tree trunk, 18°48'27"N, 98°56'37.7"E, elevation 343 m, 26 June 2023, C. Senwanna, living culture: LC10-10 = SDBR-CMU504, LC10-11 = SDBR-CMU505, and LC10-17 = SDBR-CMU506.

Ecology and distribution. Endolichenic fungi from the medulla of foliose lichen (*Parmotrema* sp.) in Thailand (this study); pathogenic as chromoblastomycosis in human in China and Mexico (Li et al. 2017; Ahmed et al. 2021), as fungal keratitis in India and USA (Ply et al. 2023; Mitra et al. 2024), as phaeohyphomycosis in France (Pruvot et al. 2023); saprobic from bamboo in China, from the environment in Japan, from plant materials in Brazil and China, and soil in China and from wheat straw in Brazil (Li et al. 2017).

Notes. A BLASTn search using ITS and *tub2* sequence data in NCBI has revealed sequence similarities of 98.98–99.83% and 98.46–99.78% between our strains (SDBR-CMU504, SDBR-CMU505, and SDBR-CMU506) and *Phialophora chinensis* strains. While the closest matches using the LSU sequence are *P. ellipsoidea* (strain MUCL 9768; AF050282) with 99.89% similarity (identities = 885/886, no gap), *P. macrospora* (strain MUCL 15541; EU514701), and *P. americana* (strain UAMH 10872; EU514691) with 99.77% similarity (identities = 864/866, no gap). The closest matches using the SSU sequence are *Capronia semiimmersa* (strain UAMH 10872; JN941209) with 99.71% similarity (identities = 1018/1021, 1 gap), *P. verrucosa* (strain AFTOL-ID 670; EF413614) with 99.60% similarity (identities = 992/996, 2 gaps), and *P. americana* (strain CBS 840.69; AY554291) with 99.33% similarity (identities = 1033/1040, 4 gaps).

In our multigene phylogenetic study, strains SDBR-CMU504, SDBR-CMU505, and SDBR-CMU506 form a clade with close affinity to *P. chinensis* (Fig. 1). However, the species segregation within the taxa is not discrete in a multigene phylogeny. Comparing the ITS, LSU, SSU, and *tub2* regions between our strains and CBS 140326 (type strain), only 1 bp difference was found in the ITS, 3 bp difference in LSU and SSU, and no base pair differences in the *tub2*. The morphology of our strains resembles the species description of *P. chinensis* provided by Li et al. (2017), except for the appearance of the conidiophores and chlamydospores and the lack of budding conidia. Although our strains have shorter conidia compared to *P. chinensis* CBS 140326, the holotype isolated from skin lesions of a human chromoblastomycosis patient (2–5 × 1.6–3.9 µm *vs* 3–6 × 2.0–5.5 µm), the detail of other structures (i.e., collarette, conidiophore, conidiogenous cells and chlamydospores) was not mentioned. Hence, an updated morphology for the species *P. chinensis* is provided.

Veronaea endolichena **Senwanna, J. Kumla & N. Suwannar., sp. nov.**
MycoBank No: 856324
Fig. 4

Etymology. Refers to the host substrate.

Type. THAILAND • Chiang Mai Province: Mueang Chiang Mai District, Suthep Subdistrict, endolichenic from the medulla of foliose lichen (*Parmotrema* sp.) on unidentified tree trunk, 18°48'27"N, 98°56'37.7"E, elevation 343 m, 26 June 2023, C. Senwanna, CMUB40068 (***Holotype***, preserved in a metabolically inactive state. ***Ex-type*** lliving culture LC10-9-2 = SDBR-CMU507).

Cultural characteristics. Colonies on different agar media were incubated in the dark at 25 °C for 2 weeks; colonies flat, irregular, with edge entire, velvety; on PDA (63 to 67 mm in diameter) surface grayish brown, dark at the middle and margin, reverse olivaceous black; on MEA (42 to 59 mm in diameter) surface brownish gray, reverse olivaceous black, producing dark brown pigment in agar; on OA (57 to 60 mm in diameter) surface brownish gray, reverse olivaceous black; on PCA (61 to 63 mm in diameter) surface and reverse brownish gray, reverse olivaceous black, sporulation absent; on CMD (54 to 55 mm in diameter) surface and reverse grayish brown; and on CMA (51 to 58 mm in diameter) surface and reverse brownish gray, sporulation absent. ***Asexual morph in vitro*** dematiaceous hyphomycetes. ***Hyphae*** 1–3.8 µm wide, subhyaline to light brown, simple to branched, septate, smooth, thin-walled, coiling observed. ***Conidiophores*** (23–)38–200(–264) × 2.3–3.7(–4.9) µm ($\bar{x}$ = 118.6 × 3.1, *n* = 25), macronematous, mononematous, erect, straight or slightly flexuous, branched, septate, cylindrical, rough-, thick-walled, light to dark brown. ***Conidiogenous cells*** (7.5–)12–102(–136.5) × 2.1–3.5(–3.9) µm ($\bar{x}$ = 53.5 × 2.9, *n* = 30), integrated, polyblastic, terminal to mostly intercalary, cylindrical, pale brown to brown, fertile parts subhyaline, rachis with crowded, flat to slightly prominent, unthickened scars. ***Conidia*** (5–)6.5–11(–13.5) × 2.5–4(–4.6) µm ($\bar{x}$ = 8.5 × 3.3, *n* = 90), solitary, cylindrical to pyriform, rounded at apex, truncate at base, lower cell longer and wider than upper one, with a prominent scar, 0.8–1.9 µm wide, pale brown, without or one median septate, constricted at the septa, smooth-walled. ***Chlamydospores*** absent. ***Sexual morph*** unknown.

Cardinal temperatures for growth on MEA after two weeks (mm). Optimum 25 °C (35 to 40), maximum 30 °C (20 to 21). No growth 4 °C and 35 °C.

Additional materials examined. THAILAND • Chiang Mai Province, Mueang Chiang Mai District, Suthep Subdistrict, endolichenic from the medulla of foliose lichen (*Parmotrema* sp.) on unidentified tree trunk, 26 June 2023, 18°48'27"N, 98°56'37.7"E, elevation 343 m, C. Senwanna, living culture LC10-2 = SDBR-CMU508 and LC10-12 = SDBR-CMU509.

Ecology and distribution. Endolichenic fungi from the medulla of foliose lichen (*Parmotrema* sp.) in Thailand.

Notes. The closet match in a BLASTn search in GenBank with the ITS, LSU, and *tub2* sequence of *V. endolichena* had highest similarity to *V. botryosa* strain GZCC:19-0557 (OP377853, with 99.65%, identities = 577/579, 2 gaps), strain CBS 127264 (MH875936, with 100%, identities = 908/908, no gap) and strain CBS 121506 (JN112502, with 93.61%, identities = 381/407, no gap), respectively. While the match using SSU sequence are *Ex. yunnanensis* (strain YMFT 1.06739; MZ781222, holotype) with 99.72% (identities = 1053/1056,

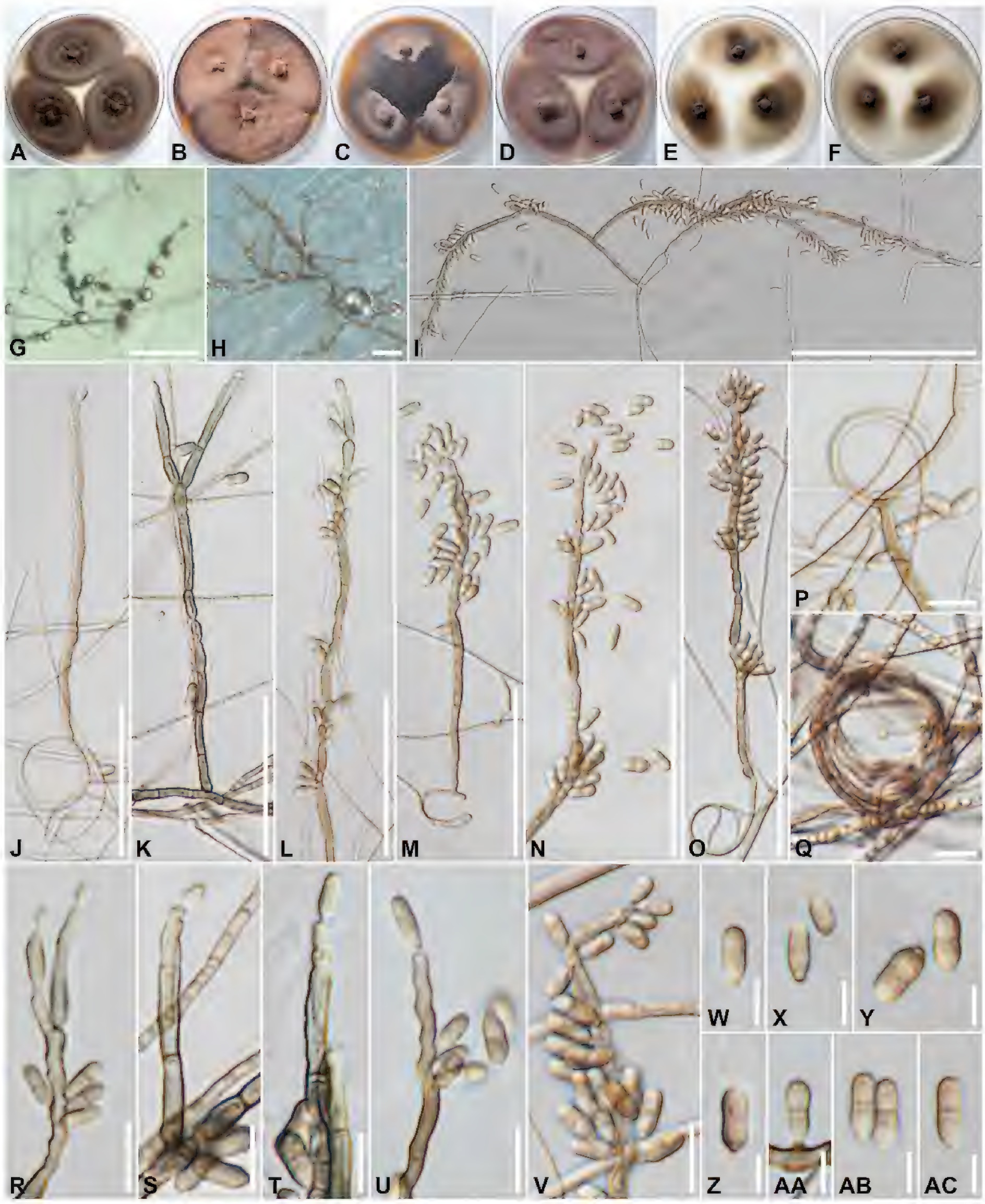

Figure 4. *Veronaea endolichena* (SDBR-CMU507, ex-type). **A–F.** Colonies on PDA, MEA, OA, PCA, CMD and CMA, respectively, after 14 d at 25 °C **G.** Conidiophores sporulating on PCA; **H.** Conidiophores sporulating on CMA; **I–O.** Conidiophores at different stages of development; **P–Q.** Hyphal coil; **R–Y.** Conidiophores with conidiogenous loci; **W–A.C** Conidia. Scale bars: 100 µm (**G–I**); 50 µm (**J–O**); 10 µm (**P–V**); 5 µm (**W–AC**).

no gap), *Thysanorea amniculi* (strain SGT69-1; OP378033, holotype) with 99.71% (identities = 1019/1022, no gap) and *Ex. aquamarine* (strain IMP-BG-H0001; MH813287) with 99.63% (identities = 1072/1076, no gap). Multigene

phylogenetic analysis of the combined dataset revealed that three strains (SDBR-CMU507, SDBR-CMU508, and SDBR-CMU509) of *V. endolichena* clustered as a sister taxon to *V. botryosa*; however, the ITS and *tub2* sequences of *V. endolichena* differ from *V. botryose* in 6 bp/610 and 25/393 bp, respectively. Morphologically, *V. endolichena* differs from *V. botryosa* in longer conidiophores, the number of septa (0–1 *vs* 0–3 septa) and size of the conidial scar (0.8–1.6 *vs* 0.5 µm) (Table 2) (Arzanlou et al. 2007, Yang et al. 2023).

Discussion

Several studies have revealed that lichen thalli host diverse microbial communities, including fungi (Oh et al. 2020; Yang et al. 2021, 2022; Diederich et al. 2022, 2024; Miral et al. 2022; Cometto et al. 2023; Si et al. 2023). Endolichenic fungi that reside inside lichens without causing any symptoms not only thrive in harsh environments but also generate unique pharmacological activities and bioactive compounds similar to those of lichens (Kellogg and Raja 2017; Singh et al. 2017; Suryanarayanan and Thirunavukkarasu 2017; Moreno et al. 2018; Agrawal et al. 2020; Yang et al. 2021; Zhang et al. 2021, 2024; Perera et al. 2022; Cometto et al. 2023). The presence of endolichenic fungi within lichen thalli suggests a symbiotic or commensal relationship, whereby these fungi enhance lichen health and resilience by producing protective secondary metabolites and potentially participating in organic matter decomposition and nutrient recycling within the thallus or its substrate (Tsurykau and Etayo 2017; Muggia and Grube 2018; Diederich et al. 2024). These functional roles may help explain the ecological success of lichens in diverse and often extreme environments, highlighting the significance of endolichenic fungi within lichen ecosystems and underscoring the need for further studies to elucidate their functions. Most endolichenic fungi have been documented from tropical areas, primarily China and India, and it is anticipated that research in other areas will yield a wealth of new species, biological compounds, and ecological data (Kellogg and Raja 2017; Suryanarayanan et al. 2017; Agrawal et al. 2020; Si et al. 2023). Recent publications have identified eight new Chaetothyriales species (*Cladophialophora endolichena*, *C. guttulate*, *C. haematommatis*, *C. heterodermiae*, *C. holoserica*, *C. olivacea*, *C. yunnanensis*, and *Paracladophialophora lichenicola*) and a new genus, *Intumescentia* in Teratosphaeriaceae, based on phylogeny and morphology and other known species in Eurotiomycetes, Dothideomycetes, and Sordariomycetes from lichen thalli (Chang et al. 2023; Cometto et al. 2023, 2024; Si et al. 2023; Diederich et al. 2024). Likewise, studies on secondary metabolites and their activities, isolated from endolichenic fungi growing in various environments, are increasing (Zhang et al. 2021; Toure et al. 2022; Varlı et al. 2022, 2023; Zhang et al. 2024). Therefore, the investigation of new ecosystems, particularly in tropical countries, is likely to reveal novel endolichenic fungi with unique potential, thereby enhancing scientific knowledge. This research employed a culture-based approach, focusing on endolichenic fungi, and is part of an ongoing study examining the diversity of endolichenic fungi in northern Thailand. Three endolichenic fungal species in Herpotrichiellaceae were identified based on morphology and phylogenetic evidence from combined datasets of ITS, LSU, SSU, and *tub2* genes.

Table 2. *Veronaea* species with a synopsis of the characteristics and relevant references.

Veronaea species	Conidiophore	Conidiogenous cells	Conidia	Sequence data	Reference
V. aquatica	Up to 280 × 2.5–4 µm. Erect, the lower part is usually straight, and the upper half is usually flexuous, usually loosely branched, sometimes geniculate, pale brown to dark brown, smooth-walled.	(3–)10–30 × 2–3.5 µm. Terminally integrated, polyblastic, occasionally intercalary, cylindrical, variable in length, pale brown, later often becoming septate, fertile part subhyaline, wide at the basal part, rachis with crowded, flat to slightly prominent, faintly pigmented; scars flat, slightly pigmented, not thickened, about 0.65 µm diam.	6–11(–12) × 2.5–3.5(–4.0) µm. Solitary, smooth, cylindrical to subpyriform and some subclavate, pale brown, most medially 1-spetate, rarely 0 or 2-septate, often constricted at the septum and the colour septum middle brown and the conidia with a round apex and truncate base; with a faintly darkened, unthickened hilum, about 0.5–0.9 µm diam.	Present	Chandrasiri et al. (2021)
V. botryosa	Up to 250 × 2–3 µm. Erect, straight or flexuose, unbranched or occasionally loosely branched, sometimes geniculate, pale brown to olivaceous brown, smooth-walled.	10–100 µm long. Terminal, occasionally intercalary, cylindrical, pale brown, later often becoming septate, fertile part subhyaline, often as wide as the basal part, rachis with crowded, flat to slightly prominent, faintly pigmented, unthickened scars.	(3–)6.5–8.5(–12) × (1.5–)2–2.5(–3) µm Solitary, smooth, cylindrical to pyriform, rounded at the apex and truncate at the base, pale brown, 1(–2)-septate, with a faintly darkened, unthickened hilum, about 0.5 µm diam.	Present	Arzanlou et al. (2007)
V. caricis	Up to 550 × 4–6 µm. Erect, straight or flexuose, sometimes swollen at the base to 10-14 µm, with numerous scars towards the apex, unbranched or occasionally loosely branched, sometimes geniculate, mid to dark brown, smooth-walled.	No information available	20–25 × 6–7 µm. Straight, fusiform or obclavate, 1 septate, hyaline or subhyaline, verruculose	Absent	Ellis (1976)
V. carlinae	Up to 130 × 2–4 µm. Simple or loosely branched, straight or flexuous, septate, pale brown, smooth, with numerous scars.	No information available	20–25 × 6–7 µm. Cylindrical, rounded at the apex and conico-truncate at the base, or fusiform, 1–3 septate, pale brown, smooth	Absent	Ellis (1976)
V. compacta	Up to 60 µm long. Slightly differentiated from vegetative hyphae, lateral or occasionally terminal, often wider than the supporting hypha, up to 4 µm wide, unbranched or branched at acute angles, with 1–3 additional septa, cells often inflated and flask-shaped, pale brown.	Up to 10 µm long. Terminal, occasionally intercalary, variable in length, cylindrical to doliiform or flask-shaped, with hardly prominent denticles, pale brown; scars flat, slightly pigmented, not thickened, about 0.5 µm diam.	(4–)6–7(–9) × 2–3 µm. Solitary, ellipsoidal to ovoid, 0–1(–2)-septate, often constricted at the septa, with a round apex and truncate base, pale brown, smooth, thin-walled; hilum prominent, slightly darkened, unthickened, about 0.5 µm diam.	Present	Arzanlou et al. (2007)
V. coprophila	Up to 350 × 3–4.5 µm. Straight or flexuous, septate, mid to dark brown, paler towards the apex where there are a number of small, flat scars.	No information available	6–12 × 3–5 µm. Straight, cylindrical, rounded at the apex, conico-truncate at the base or ellipsoidal, 1–2 septate, smooth, pale brown.	Absent	Ellis (1976)
V. endolichena	(23–)38–200(–264) × 2.3–3.7(–4.9) µm. Erect, straight or slightly flexuous, branched, septate, cylindrical, light to dark brown, rough-, thick-walled.	(7.5–)12–102(–136.5) × 2.1–3.5(–3.9) µm. Integrated, polyblastic, terminal to mostly intercalary, cylindrical, pale brown to brown, fertile parts subhyaline, rachis with crowded, flat to slightly prominent, unthickened scars.	(5–)6.5–11(–13.5) × 2.5–4(–4.6) µm. Solitary, cylindrical to pyriform, rounded at apex, truncate at base, lower cell longer and wider than upper one, with a prominent scar, 0.8–1.9 µm wide, pale brown, without or one median septate, constricted at the septa, smooth-walled.	Present	This study
V. ficina	30–120 × 2.5–4.75 µm. Superficial, arising singly as lateral or terminal branches from external hyphae ranging from macronematous to mononematous, erect, straight to flexuous or slightly curved, smooth-walled, unbranched, septate with brown base and paler apex.	Integrated, polyblastic, terminal to predominantly intercalary, sympodial, cylindrical, cicatrized with thickened scars.	4.5–18.5 × 5.5 µm. Holoblastic, dry, simple, not catenate, finely verruculose, obovoidal, base obconicotruncate, apex rounded, 0–3-septate, pale brown.	Absent	Kharwar and Singh (2004)
V. filicina	400–800 × 2–2.5 µm. Base rarely swollen, rarely branched, sparsely septate, at first thin-walled, roughened walls, olivaceous then to brown.	No information available	6–13.5 × 3–4 µm. Elliptical or pyriform, not constricted at septa, 1–3- septate, olivaceous or fuscous.	Absent	Dingley (1972)
V. gobica	Up to 350 × 1.5–2.5 µm. Straight or flexuous, septate, smooth, with numerous minute scars towards the apex, brown.	No information available	4–6.5 × 2–3.5 µm. Ellipsoid, smooth, Subhyaline or pale brown	Absent	Pan and Zhang (2009)
V. grewiicola	42–104 × 2.5–6.3 µm. Sometimes curved, smoothwalled, branched, 2–5 septa, pale brown to brown base and paler apex.	Integrated, polyblastic, terminal to mostly intercalary, sympodial and cicatrized with thickened scars.	7.3–19.5 × 2.6–7.5 µm. Holoblastic, dry, simple, non-catenate, finely verruculose, sometimes constricted at the septa, hilum thickened with truncate base and rounded apex, 0–2(–3) septate subhyaline or pale brown	Absent	Kharwar and Singh (2004)

Veronaea species	Conidiophore	Conidiogenous cells	Conidia	Sequence data	Reference
V. hedychii	19.5–86.5 × 2.5–3.5 µm. Sometimes with an inflated base up to 7 µm diam., straight to slightly curved, unbranched, 1–6 septate, golden brown to brown, paler towards the apices, smooth.	10–40 × 1.5–2.5 µm. Terminal, holoblastic, sometimes intercalary, densely and minute cicatrized, scars thickened, 1 µm wide.	5–10 × 2–4 µm. Ellipsoid, cylindrical or obovoid, base obconic truncate, apex rounded, 0–1 septate, sometimes slightly constricted at the septum, subhyaline to pale brown, smooth, hila thickened, somewhat darkened, 1 µm diam.	Absent	Soares and Barreto (2008)
V. hippocrateae	27–123 × 2–4 µm. Straight to slightly curved, unbranched, paler towards the apices, 1–6 septate, smooth, brown to dark brown.	No information available	4–18.5 × 1.5–3.5 µm, Solitary, non-catenate, smooth-walled, obconico base, apex rounded, 0–1-septate, cylindric to obclavate, slightly curved, subhyaline to pale brown	Absent	Kharwar and Singh (2004)
V. japonica	Up to 65 × 2–3 µm. Slightly differentiated from aerial vegetative hyphae, lateral, or terminal, often wider than the supporting hypha, unbranched or occasionally branched, pale brown, thin-walled, smooth, with 1–3 additional septa.	Up to 15 µm long. Terminal, occasionally intercalary, variable in length, pale brown, cylindrical to clavate, with hardly prominent denticles; scars flat, slightly pigmented, not thickened, about 0.5 µm diam.	(6–)7–8(–10) × 2–2.5(–4) µm. Solitary, pale brown, smooth, thin-walled, ellipsoidal to ovoid, (0–)1-septate, often constricted at the septum, with a round apex and truncate base; hilum unthickened but slightly darkened, about 1 µm diam.	Present	Arzanlou et al. (2007)
V. latispora	Up to 90 × 1.5–2.5 µm. Straight or slightly curved, septate, smooth, with numerous minute scars at the upper parts, brown.	No information available	7.5–9.5 × 3–5 Broadly obovoid, smooth, aseptate, subhyaline to pale brown.	Absent	Pan and Zhang (2009)
V. oblongispora	Up to 320 × 3–5 µm. Solitary or sometimes in fascicles, smooth, bulbous towards the base, pale brown to brown.	No information available	7–8 × 4–5 µm. Oblong, smooth, aseptate, rather thick-walled, obtuse at the apex, subhyaline to pale brown.	Absent	Morgan-Jones (1982)
V. polyconidia	1125–1515 × 45–70 µm. Straight or slightly flexuous, unbranched, solitary, cylindrical, rough-walled, thick-walled, brown to dark brown.	Polyblastic, terminal, cylindrical, rachis with crowded, flat to slightly prominent, pale brown, fertile parts subhyaline.	11–16 × 3–5 µm. Solitary and smooth, cylindrical to pyriform, rounded at apex and truncate at base, pale brown, 1–3-septate (mostly 3), often constricted and medium brown at septa.	Present	Su et al. (2023)
V. queenslandica	No information available	No information available	No information available	Absent	Matsushima (1989); Index Fungorum (2025)
V. smilacis	70–165 (–90–125) × 3.5–5.5 µm. Solitary, thick-walled, smooth, up to 12-septa, brown.	No information available	21.5–32.5 × 2–5 µm. Solitary, cylindrical to slightly obclavate, 1–12 septate, smooth-walled, subhyaline to pale olivaceous.	Absent	Singh et al. (1981)
V. tectonae	Up to 200 × 3.6 µm. Solitary smooth, up to 10-septa, pale brown.	No information available	11 × 3.75 µm. Solitary, simple, smooth, usually 1-septa, prominent scars at the base.	Absent	Kamal (1980)
V. thylacospermi	35–100 × 3–4 µm. Simple, smooth, brown, 1–3(–8) septate, basal cell inflated 6–10 µm wide, fertile part taller than basal part, forming slightly flexuous rachis with scattered, hyaline and small, apically pointed denticle-like.	Conidiogenous loci 0.3 µm high, 0.5 µm wide.	12–14 × 3–4 µm. Two-celled, lower cell longer and wider than upper one, wall slightly verruculose, hyaline to pale brown.	Absent	Chlebicki (2009)

Atrokylindriopsis was established by Ma et al. (2015) to accommodate the single species *At. setulosa*. *Atrokylindriopsis setulosa* was reported as saprobic on dead branches of an unidentified broadleaf tree and was placed in Chaetothyriales without a family assigned, based on a BLASTn search using ITS and LSU sequence data from NCBI and morphological comparisons (Ma et al. 2015). Wijayawardene et al. (2020) considered this genus to be in the Chaetothyriales, but later Quan et al. (2020) assigned it to the Herpotrichiellaceae. Morphologically, the pigmented, septate, setulate conidia are a unique feature of *Atrokylindriopsis*, distinguishing it from other members of Herpotrichiellaceae. In the present phylogenetic tree (Fig. 1), the new species, *At. racemosospora*, is closely related to *At. setulosa*. *Atrokylindriopsis racemosospora* exhibits morphological differences from *At. setulosa*, as mentioned above. Based on morphology, *At. racemosospora* might represent a different genus from *Atrokylindriopsis*. The holotype (HMAS245592) and dried culture specimens

(HSAUP H4560) of *At. setulosa* were not reexamined, as they had been lost. Consequently, it was not possible to reassess the morphology. Due to the similarity in the ITS and LSU sequences between *At. racemosospora* and *At. setulosa*, along with the unavailability of protein-coding gene sequence data of *At. setulosa*, it was deemed insufficient evidence to justify separating them into different genera. Since the molecular data were unclear in resolving the relationships between *At. setulosa* and our specimens, we tentatively classified our strains as a new species within *Atrokylindriopsis*. Additionally, the examination of newly collected specimens, morphology, and molecular data regarding protein-coding genes of *At. setulosa* requires further study. It is worth noting that *At. racemosospora* is similar to *Aciculomyces* and *Petriomyces* in having sympodial conidiogenous cells that produce conidia from short denticles and obovoid, aseptate conidia (Thitla et al. 2023; Torres-Garcia et al. 2023). Based on morphological characters and multi-gene phylogenetic analysis, *Aciculomyces* was established by Torres-Garcia et al. (2023) to accommodate the single species *Ac. restrictus*, collected from fluvial sediments, while *Petriomyces*, typified by *P. obovoidisporus*, was isolated from sandstone in a natural forest (Thitla et al. 2023). Moreover, *At. racemosospora* can be distinguished from these genera by the abundance of sporulation, inconspicuous conidial scars, and the phylogenetic analysis, which also segregates these genera.

Phialophora is known as a group of black yeasts and their relatives, which have been reported as pathogens in humans and animals, as well as saprobic and endophytic in plant materials and soil (Schol-Schwarz 1970; Untereiner et al. 2008; Liu et al. 2013; Li et al. 2017). The genus is typified by *P. verrucosa* and characterized by pigmented hyphae, solitary or aggregated conidiophores, cylindrical to flask-shaped phialides bearing conspicuous, darkly pigmented collarettes, and ovoid to cylindrical, aseptate conidia (Medlar 1915; Schol-Schwarz 1970; Gams 2000; Untereiner et al. 2008). Currently, 38 epithets are listed for *Phialophora* in Index Fungorum (2025). Morphology alone is insufficient for species identification within *Phialophora*; moreover, molecular data have demonstrated significant genetic variation within the species complex, now referred to as the *P. verrucosa* species complex (Li et al. 2017). Several species have been transferred to other genera, such as *Chloridium*, *Cyphellophora*, *Entimomentora*, *Hyphodiscus*, *Lasiosphaeris*, and *Rhopalophora*, based on morpho-molecular analyses (Bogale et al. 2010; Réblová et al. 2011, 2013, 2017; Johnston et al. 2014; Untereiner et al. 2019). Although many sequences of *Phialophora* are available in GenBank, in our pre-analyses, *P. asteris*, *P. asteris* f. sp. *helianthi*, *P. atrovirens*, *P. avicenniae*, *P. cinerescens*, *P. cyclaminis*, *P. dancoi*, *P. foetens*, *P. intermedia*, *P. japonica*, and *P. mustea* were grouped outside of the clade comprising members of Herpotrichiellaceae. Therefore, we excluded these sequences from our analysis. Our molecular phylogenetic tree indicated that our three strains formed a separate clade within the *P. chinensis* clade, with representative strains of *P. chinensis* separated into two subclades, supported by 86% ML and 1 PP statistical support (Fig. 1). Sequence comparisons of ITS, LSU, SSU, and *tub2* genes between our strains and representative strains from two sub-clades indicate that our strains are congeneric. The conidial size of our strains aligns well with *P. chinensis*; however, the dematiaceous hyphomycetes of our strains cannot be directly compared with the type, as Li et al. (2017) did not provide a detailed description of conidiophores, conidiogenous cells,

collarettes, and chlamydospores. According to Li et al. (2017), *P. chinensis* has been isolated from human patients, leaves, soil, wheat straw, and wood, which may account for morphological variation within the species. Based on the available data, we identified our strains as *P. chinensis*, which were collected as endolichenic fungi associated with foliose lichens in Thailand. *Phialophora* identification was initially based on morphology and molecular phylogeny (Yan et al. 1995; de Hoog et al. 1999; Untereiner et al. 2008). Although similar conidia can be observed among *Phialophora* species, genetic variation in the ITS, LSU, and *tub2* gene regions can be used to distinguish species. However, since most available sequences of *P. chinensis* contain only three gene regions and excluded species contain only the ITS gene region, species delineation based on phylogeny remains uncertain. Therefore, more informative genes (i.e., *act*, *tef1*, and *rpb2*) and additional collections may help clarify species placement and reveal the possibility of a species complex.

Veronaea was introduced by Ciferri and Montemartini (1957) and is typified by *V. botryose*. There are 20 epithets recorded in Index Fungorum (2025), but only five species have been identified with DNA sequence data. Based on multigene analyses and morphological comparisons, *V. constricta* (CBS 572.90, type strain) has been considered a synonym of *V. botryosa* (Su et al. 2023; Yang et al. 2023). In our phylogenetic tree, the *Veronaea* species clusters as a monophyletic clade (Fig. 1), maintaining a stable position within Herpotrichiellaceae, which concurs with the findings of Su et al. (2023) and Yang et al. (2023). *Veronaea endolichena* is introduced based on phylogenetic analysis and morphological data. A morphological comparison between *V. endolichena* and other *Veronaea* species is shown in Table 2. *Veronaea endolichena* is similar to *V. caricis*, *V. compacta*, *V. hedychii*, *V. hippocrateae*, *V. japonica*, *V. tectonae*, and *V. thylacospermi* in having 0–1-septate conidia. However, the conidia of *V. compacta* (4–9 × 2.5–4 µm), *V. hedychii* (5–10 × 2–4 µm), *V. japonica* (6–10 × 2–4 µm) and *V. tectonae* (11 × 3.75 µm) are shorter than those of *V. endolichena* (5–13.5 × 2.5–4.6 µm) (Ellis 1976; Kamal 1980; Kharwar and Singh 2004; Arzanlou et al. 2007; Soares and Barreto 2008; Chlebicki 2009). *Veronaea caricis* (20–25 × 6–7 µm) and *V. hippocrateae* (4–18.5 × 1.5–3.5 µm) have longer conidia than *V. endolichena* (Ellis 1976; Kharwar and Singh 2004). *Veronaea endolichena* (5–13.5 × 2.5–4.6 µm) is closely related to *V. thylacospermi* (12–14 × 3–4 µm); however, *V. endolichena* has longer conidiophores (23–264 × 2.3–4.9 µm *vs* 35–100 × 3–4 µm) and cylindrical to pyriform, smooth-walled conidia (Chlebicki 2009). Based on both morphological characteristics and multigene analyses, a novel species is introduced. Phylogenetically, *E. brunnea* (CBS 587.66) also clustered within the *Veronaea* clade (Fig. 1), which concurred with the results conducted by Costa et al. (2023) and Torres-Garcia et al. (2023). *Exophiala brunnea* differs from *Veronaea* in its conidiophores and phialides (Papendorf 1969; de Hoog et al. 2011); therefore, it was maintained as a separate species pending further investigation. Most species of *Veronaea* are known to be saprobes on various hosts worldwide (Arzanlou et al. 2007; Soto et al. 2017; Chandrasiri et al. 2021; Su et al. 2023; Yang et al. 2023). Since *Veronaea* exhibits overlapping characteristics, species delimitation based solely on morphology is challenging (Su et al. 2023); therefore, additional sampling is necessary for further investigation.

Our phylogenetic analyses indicated that *Capronia*, *Cladophialophora*, *Exophiala*, *Fonsecaea*, and *Rhinocladiella* are polyphyletic within the family

Herpotrichiellaceae, which is concurred with Teixeira et al. (2017), Thitla et al. (2023), and Torres-Garcia et al. (2023). Whereas *Aciculomyces*, *Aculeata*, *Atrokylindriopsis*, *Marinophialophora*, *Melanoctona*, *Petriomyces*, *Phaeoannellomyces*, *Phialophora*, *Thysanorea*, *Uncispora*, *Valentiella*, and *Veronaea* represent a monophyletic group. Considering the asexual morph resemblance together with molecular support, Hernández-Restrepo et al. (2020) treat most *Minimelanolocus* species under *Thysanorea*. Although several species of *Minimelanolocus* have been recently reported based on morphological characteristics, these species lack sequence data, including the type species (Costa et al. 2018; Barreto et al. 2024). *Pleomelogramma* is also considered a doubtful genus in Herpotrichiellaceae, pending further studies due to the lack of sequence data for the type species. (Quan et al. 2020). Based on molecular analyses with distinctive ecological trends, de Hoog et al. (2011) defined the members of this family into six clades: *bantiana-*, *carrionii-*, *salmonis-*, *europaea-*, *dermatitidis-*, and *jeanselmei-* clades. With morphology and multi-gene phylogeny analyses, the species in the europaea clade were assigned as members of Cyphellophoraceae (Réblová et al. 2013). According to Wijayawardene et al. (2022), *Brycekendrickomyces*, *Metulocladosporiella*, *Neosorocybe*, and *Sorocybe* had previously been classified within Herpotrichiellaceae. However, the phylogenetic position of *Brycekendrickomyces* and *Metulocladosporiella* was presented in Trichomeriaceae (Quan et al. 2020, 2024). The ITS and LSU phylogenetic analyses by Quan et al. (2024) revealed that *Neosorocybe* and *Sorocybe* are separate from the Herpotrichiellaceae clade, forming a sister clade to the Epibryaceae clade in Chaetothyriales. Later, Thitla et al. 2023 treated both genera in Chaetothyriales *incertae sedis*.

Munk (1953) defined the characteristics of anamorphic Herpotrichiellaceae as dematiaceous hyphomycetes (black yeast), typified by proliferating, percurrently conidiogenous cells, conidiogenesis with holoblastic conidia produced from minute pegs or denticles, and unicellular conidia often held in chains. It is worth noting that several obligate lichenicolous Herpotrichiellaceae genera, such as *Cladophialophora*, have been found on lichen thalli or apothecia. These species differ from others in forming minute conidiophores in sporodochia, and in some species, two distinct types of conidia are observed (Diederich et al. 2024). A few species, such as *Aculeata aquatica*, *Atrokylindriopsis setulosa*, and *Melanoctona tectonae*, can also be distinguished from other Herpotrichiellaceae species by their conidiogenesis and conidial morphology (Ma et al. 2015; Tian et al. 2016; Dong et al. 2018). Although ITS and LSU sequence analyses support the placement of these three species in Herpotrichiellaceae, reliable genes (e.g., *rpb2*, *tef1*, and *tub2*) may provide better resolution for distinguishing species within this family. Due to the recent increase in the number of Herpotrichiellaceae members and the apparent polyphyletic nature of their characteristics, the delineation of the family remains inconclusive (Tian et al. 2021; Crous et al. 2023). Currently, most sequence data of Herpotrichiellaceae strains in GenBank are available only for ribosomal genes, including ITS, LSU, and SSU, while data for protein-coding genes remain limited. Although the ITS and LSU can be used for linking sexual and asexual morphs and delimitating species, their classification is often unclear or placed in unsupported branches (Untereiner and Naveau 1999; Quan et al. 2020, 2022; Costa et al. 2023; Thitla et al. 2023; Torres-Garcia et al. 2023). Polyphyletic genera (i.e., *Capronia*, *Cladophialophora*, *Exophiala*, *Fonsecaea*, and *Rhinocladiella*) and ambiguous species within the Herpotrichiellaceae family are still waiting for resolution,

particularly with the inclusion of newly collected specimens. Likewise, sequences of protein-coding genes (e.g., *act*, *rpb2*, *tef1*, and *tub2*) from additional collections, as well as the re-sequencing of generic types within this family and polyphyletic strains, are required to clarify their phylogenetic affinity and species delineation.

Members of the family Herpotrichiellaceae play various ecological roles, including endophytic, epiphytic, fungicolous, hypersaprobic, lichenicolous, pathogenic, rock-inhibiting, and saprobic taxa, on different substrates, as listed in Table 3. These fungi not only interact with their hosts in various ways but are also considered opportunistic organisms that inhabit natural environments (Crous et al. 2007; Quan et al. 2024). Members of the family Herpotrichiellaceae are known

Table 3. Updated genera in Herpotrichiellaceae with their life mode, habitat, and isolation sources.

Genera	Life mode	Habitat	Isolation source	References
Aciculomyces	Saprobic	Freshwater	Fluvial sediments	Torres-Garcia et al. (2023)
Aculeata	Saprobic	Freshwater	Submerged wood	Dong et al. (2018)
Atrokylindriopsis	Saprobic and endolichenic	Terrestrial	Dead branches of an unidentified broadleaf tree and lichen (*Parmotrema* sp.)	Ma et al. (2015); this study
Capronia	Epiphytic, fungicolous and hypersaprobic, lichenicolous, and saprobic	Terrestrial	Fungi, lichen, litter, plants, soil, water, and wood	Müller et al. (1987); Etayo (2002); Untereiner (2000); Untereiner and Naveau (1999); Untereiner et al. (2011); Marincowitz et al. (2008); Teixeira et al. (2017); Phookamsak et al. (2019); Sánchez et al. (2019); Roux et al. (2020); Hollinger and Lendemer (2021); Tian et al. (2021)
Cladophialophora	Endophytic, fungicolous lichenicolous, pathogenic, rock-inhabiting, and saprobic	Terrestrial and freshwater	Fluvial sediments, lichen, plants, rock, sawdust, soil, wood, warm-blooded animal, and water	Teixeira et al. (2017); Quan et al. (2020); Thitla et al. (2023, 2024); Chang et al. (2023); Cometto et al. (2023)
Exophiala	Endophytic, fungicolous, pathogenic, rock-inhabiting, and saprobic	Aquatic, marine, and terrestrial	Cold blooded animals, fungi, litter, plants, rock, sediments, soil, various substrates (i.e., contact lens, plastic foil, soap container, etc.), warm-blooded animals, and water	de Hoog et al. (2011); Teixeira et al. (2017); Quan et al. (2020); Tian et al. (2021); Thitla et al. (2022); Ide-Pérez et al. (2024)
Fonsecaea	Epiphytic, pathogenic, and saprobic	Terrestrial	Cold blooded animal, insect, lichen, litter, plants, soil, warm-blooded animal, and wood	Vicente et al. (2012, 2014); de Azevedo et al. (2015); Teixeira et al. (2017); de Souza Lima et al. (2020); Sousa et al. (2024)
Marinophialophora	Saprobic	Marine	Associated with *Halocyphina* species on decaying mangrove wood	Li et al. (2018)
Melanoctona	Saprobic	Terrestrial	Decaying wood	Tian et al. (2016)
*Minimelanolocus**	Saprobic	Aquatic and terrestrial	Litter, plants, and submerged wood	Castañeda Ruíz et al. (2001, 2003); Zhang et al. (2009); Ma et al. (2011); Heredia et al. (2014); Hernández-Restrepo et al. (2013); Tian et al. (2016)
Petriomyces	Rock-inhabiting	Terrestrial	Rock	Thitla et al. (2023)
Phialophora	Endolichenic, pathogenic, and saprobic	Freshwater and terrestrial	Cold blooded animal, fluvial sediments, food, lichen, plants, soil, warm-blooded animal, water, and wood	Li et al. (2017); Jiang et al. (2017); Song et al. (2021); Tian et al. (2021); Ply et al. (2023); Torres-Garcia et al. (2023); **this study**
Phaeoannellomyces	Pathogenic	Terrestrial	Warm-blooded animal	McGinnis et al. (1985)
*Pleomelogramma**	Saprobic	Terrestrial	Decaying woody plants	Spegazzini (1909)
Rhinocladiella	Epilithic, epiphytic, lichenicolous, pathogenic, and saprobic	Terrestrial	Honey, insects, plants, soil, warm-blooded animal, and wood	Arzanlou et al. (2007); Hernández-Restrepo et al. (2016); Teixeira et al. (2017); de Souza Lima et al. (2020); Quan et al. (2020); Roeun et al. (2022); Sousa et al. (2024)
Thysanorea	Saprobic	Aquatic and terrestrial	Plants and wood	Arzanlou et al. (2007); Tian et al. (2016); Dong et al. (2018); Hernández-Restrepo et al. (2020); Yang et al. (2023)
Uncispora	Saprobic	Freshwater and terrestrial	Plants and submerged wood	Sinclair and Morgan-Jones (1979); Li et al. (2014); Liu et al. (2018)
Valentiella	Saprobic	Terrestrial	Carton runway galleries built by *Azteca brevis* ants and plants	Nepel et al. (2014); Bezerra et al. (2022)
Veronaea	Endophytic, epiphytic, pathogenic, and saprobic	Freshwater and terrestrial	Animal dung, cold-blooded animal, plants, soil, warm blooded animal, and wood	Ellis (1976); Papendorf (1976); Moustafa and Abdul-Wahid (1990); Arzanlou et al. (2007); Soares and Barreto (2008); Chlebicki (2009); Sang et al. (2011) Soto et al. (2017) Coleman et al. (2018); Chandrasiri et al. (2021); Su et al. (2023); Yang et al. (2023); **this study**

* Sequence data are not available.

for their biochemical and ecological adaptations that enable survival in extreme environments, often linked to the production of protective compounds such as melanin (de Hoog et al. 2011; Zhan et al. 2011; Coleine and Selbmann 2021; Coelho et al. 2022; Quan et al. 2024; de León et al. 2025). For example, *Cladophialophora exuberans*, *Exophiala dermatitidis*, *E. pisciphila*, and *E. phaeomuriformis* produce melanin, which enables them to thrive under high-radiation, high-temperature or oligotrophic conditions (Badali et al. 2008; de Hoog et al. 2011; Zhan et al. 2011; Cordero and Casadevall 2017; Benmessaoud et al. 2023; da Silva et al. 2023; de León et al. 2025). Although this study employed culture-based techniques to isolate and identify endolichenic fungi within Herpotrichiellaceae, many taxa from this family and others likely remain undetected due to their unculturable nature, low abundance, or specific growth requirements. Future research incorporating metaomics approaches, including metagenomics and metatranscriptomics, could provide a more comprehensive view of fungal diversity, functional gene expression, and ecological interactions within the lichen holobiont. These tools offer promising avenues to uncover hidden fungal lineages and understand their metabolic roles in lichen symbiosis and environmental adaptation.

Acknowledgements

The authors are grateful to Hatthakom Mingrujidith and Nopparat Wannathes for their kind advice in naming the new fungal taxa. Liwei Zhou, Nalin N. Wijayawardene, Rungtiwa Phookamsak, and Ausana Mapook are gratefully acknowledged for their valuable suggestions and help.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

Nakarin Suwannarach and Chanokned Senwanna expresses appreciation to the CMU Proactive Researcher Program, Chiang Mai University.

Author contributions

Conceptualization: CS, NS. Data curation: CS, JK, PK, ND, NS. Formal analysis: CS, JK, NS. Funding acquisition: CS,NS. Investigation: CS, JK, NS. Methodology: CS, NS. Project administration: NS. Software: CS, JK. Supervision: JK, NS. Validation: CS, JK, NS. Visualization: CS, JK, NS. Writing – original draft: CS, JK, NS. Writing – review & editing: CS, JK, PK, ND, NS.

Author ORCIDs

Chanokned Senwanna https://orcid.org/0000-0002-1008-4514
Jaturong Kumla https://orcid.org/0000-0002-3673-6541

Pratthana Kodchasee https://orcid.org/0000-0003-0432-4910
Nutchanan Duangkon https://orcid.org/0009-0008-5769-0117
Nakarin Suwannarach https://orcid.org/0000-0002-2653-1913

Data availability

All of the data that support the findings of this study are available in the main text.

References

Agrawal S, Deshmukh SK, Reddy MS, Prasad R, Goel M (2020) Endolichenic fungi: A hidden source of bioactive metabolites. South African Journal of Botany 134: 163–186. https://doi.org/10.1016/j.sajb.2019.12.008

Ahmed SA, Bonifaz A, González GM, Moreno LF, Menezes da Silva N, Vicente VA, Li R, de Hoog S (2021) Chromoblastomycosis Caused by *Phialophora*—Proven Cases from Mexico. Journal of Fungi 7: e95. https://doi.org/10.3390/jof7020095

Arnold AE, Miadlikowska J, Higgins KL, Sarvate SD, Gugger P, Way A, Hofstetter V, Kauff F, Lutzoni FA (2009) Phylogenetic estimation of trophic transition networks for ascomycetous fungi: Are lichens cradles of symbiotrophic fungal diversification? Systematic Biology 58: 283–297. https://doi.org/10.1093/sysbio/syp001

Arzanlou M, Groenewald JZ, Gams W, Braun U, Crous PW (2007) Phylogenetic and morphotaxonomic revision of *Ramichloridium* and allied genera. Studies in Mycology 58: 57–93. https://doi.org/10.3114/sim.2007.58.03

Badali H, Gueidan C, Najafzadeh MJ, Bonifaz A, van den Ende AH, de Hoog GS (2008) Biodiversity of the genus *Cladophialophora*. Studies in Mycology 61: 175–191. https://doi.org/10.3114/sim.2008.61.18

Bamrungpanichtavorn T, Ungwiwatkul S, Boontanom P, Chantarasiri A (2023) Diversity and cellulolytic activity of cellulase-producing bacteria isolated from the soils of two mangrove forests in Eastern Thailand. Biodiversitas Journal of Biological Diversity 24: 3891–3902. https://doi.org/10.13057/biodiv/d240728

Barreto GG, Cantillo-Pérez T, Primo de Souza MGA, Castañeda-Ruiz RF, Gusmão LFP (2024) Observations on the genus *Minimelanolocus*, allied with descriptions of new genera, species, synonyms and new combinations. New Zealand Journal of Botany 63(4): 688–703. https://doi.org/10.1080/0028825X.2024.2404120

Benmessaoud S, Anissi J, Kara M, Assouguem A, Gaga Y, Ajdi M, Ullah R, Ali EA, Ercisli S, Fidan H, Kaur S (2023) Melanin antibacterial activity of two new strains, SN1 and SN2, of *Exophiala phaeomuriformis* against five human pathogens. Open Chemistry 21: e20230182. https://doi.org/10.1515/chem-2023-0182

Bezerra JDP, Navarro HMC, Almeida JH, Félix CR, Landell MF (2022) *Valentiella maceioensis* gen. et sp. nov. (Herpotrichiellaceae, Chaetothyriales), a new black yeast-like fungus isolated from bromeliads in Brazil. Mycological Progress 21: e30. https://doi.org/10.1007/s11557-022-01783-3

Bogale M, Orr MJ, O'Hara MJ, Untereiner WA (2010) Systematics of *Catenulifera* (anamorphic Hyaloscyphaceae) with an assessment of the phylogenetic position of *Phialophora hyalina*. Fungal Biology 114: 396–409. https://doi.org/10.1016/j.funbio.2010.02.006

Buaruang K, Boonpragob K, Mongkolsuk P, Sangvichien E, Vongshewarat K, Polyiam W, Rangsiruji A, Saipunkaew W, Naksuwankul K, Kalb J, Parnmen S, Kraichak E, Phraphuchamnong P, Meesim S, Luangsuphabool T, Nirongbut P, Poengsungnoen V, Duangphui N, Sodamuk M, Phokaeo S, Molsil M, Aptroot A, Kalb K, Lücking R, Lumbsch HT

(2017) A new checklist of lichenized fungi occurring in Thailand. MycoKeys 23: 1–91. https://doi.org/10.3897/mycokeys.23.12666

Casale M, Bagnasco L, Giordani P, Mariotti MG, Malaspina P (2015) NIR spectroscopy as a tool for discriminating between lichens exposed to air pollution. Chemosphere 134: 355–360. https://doi.org/10.1016/j.chemosphere.2015.03.095

Castañeda Ruíz RF, Heredia G, Reyes M, Arias RM, Decock C (2001) A revision of the genus *Pseudospiropes* and some new taxa. Cryptogamie. Mycologie 22: 3–18. https://doi.org/10.1016/S0181-1584(01)01057-0

Castañeda Ruíz RF, Guarro J, Velásquez-Noa S, Gené J (2003) A new species of *Minimelanolocus* and some hyphomycete records from rain forests in Brazil. Mycotaxon 85: 231–239.

Chakarwarti J, Nayaka S, Srivastava S (2020) Diversity of endolichenic fungi – A review. Asian Journal of Mycology 3: 490–511. https://doi.org/10.5943/ajom/3/1/18

Chandrasiri SKU, Liu YL, Huang JE, Samarakoon MC, Boonmee S, Calabon MS, Hu DM (2021) *Veronaea aquatica* sp. nov. (Herpotrichiellaceae, Chaetothyriales, Eurotiomycetes) from submerged bamboo in China. Biodiversity Data Journal 9: e64505. https://doi.org/10.3897/BDJ.9.e64505

Chang R, Wang Y, Liu Y, Wang Y, Li S, Zhao G, Zhang S, Dai M, Zheng X, Bose T, Si H (2023) Nine new species of black lichenicolous fungi from the genus *Cladophialophora* (Chaetothyriales) from two different climatic zones of China. Frontiers in Microbiology 14: e1191818. https://doi.org/10.3389/fmicb.2023.1191818

Chlebicki A (2009) Fungi on higher plants of the upper limit of the alpine zone: New species from Tian Shan. Mycotaxon 110: 443–450. https://doi.org/10.5248/110.451

Ciferri R, Montemartini A (1957) Sui generi Muchmoria Sacc. e *Veronaea* n.gen. (Dematiaceae, Didymosporae). Atti dell'Istituto Botanico della Università e Laboratorio Crittogamico di Pavia 15: 67–72.

Coelho RA, Figueiredo-Carvalho MHG, Silva JVdS, Correa-Junior D, Frases S, Zancopé-Oliveira RM, Freitas DFS, Almeida-Paes R (2022) Does DHN-Melanin Always Protect Fungi against Antifungal Drugs? The *Fonsecaea*/Micafungin Paradigm. Microbiology Research 13: 201–209. https://doi.org/10.3390/microbiolres13020017

Coleine C, Selbmann L (2021) 2.1 Black Fungi Inhabiting Rock Surfaces. In: Büdel B, Friedl T (Eds) Life at Rock Surfaces: Challenged by Extreme Light, Temperature and Hydration Fluctuations. De Gruyter, Berlin/Boston, 57–86. https://doi.org/10.1515/9783110646467-003

Coleman DJ, Camus AC, Martínez-López B, Yun S, Stevens B, Soto E (2018) Effects of temperature on *Veronaea botryosa* infections in white sturgeon *Acipenser transmontanus* and fungal induced cytotoxicity of fish cell lines. Veterinary Research 49: e11. https://doi.org/10.1186/s13567-018-0507-0

Cometto A, Leavitt SD, Grube M, de Hoog S, Muggia L (2023) Tackling fungal diversity in lichen symbioses: Molecular and morphological data recognize new lineages in Chaetothyriales (Eurotiomycetes, Ascomycota). Mycological Progress 22: e53. https://doi.org/10.1007/s11557-023-01901-9

Cometto A, Ametrano CG, de Carolis R, Leavitt SD, Grube M, Pallavicini A, Muggia L (2024) Highly heterogeneous mycobiota shape fungal diversity in two globally distributed lichens. Fungal Ecology 69: e101331. https://doi.org/10.1016/j.funeco.2024.101331

Cordero RJ, Casadevall A (2017) Functions of fungal melanin beyond virulence. Fungal Biology Reviews 31: 99–112. https://doi.org/10.1016/j.fbr.2016.12.003

Costa PM, Malosso E, Barbosa MA, Tavares WL, Castaneda-Ruiz RF (2018) *Minimelanolocus atlanticus* sp. nov. and *M. navicularis* from the Brazilian Atlantic Forest. Mycotaxon 132: 925–931. https://doi.org/10.5248/132.925

Costa FDF, Souza RSD, Voidaleski MF, Gomes RR, Reis GF, Lima BJDS, Candido GZ, Geraldo MR, Soares JM, Schneider GX, Trindade EDS (2023) Sugarcane: An unexpected habitat for black yeasts in Chaetothyriales. IMA Fungus 14: e20. https://doi.org/10.1186/s43008-023-00124-7

Crawford SD (2019) Lichens Used in Traditional Medicine. In: Ranković B (Ed.) Lichen Secondary Metabolites. Springer Nature, Switzerland, 31–97. https://doi.org/10.1007/978-3-030-16814-8_2

Crous PW, Schubert K, Braun U, de Hoog GS, Hocking AD, Shin HD, Groenewald JZ (2007) Opportunistic, human-pathogenic species in the Herpotrichiellaceae are phenotypically similar to saprobic or phytopathogenic species in the Venturiaceae. Studies in Mycology 58: 185–217. https://doi.org/10.3114/sim.2007.58.07

Crous PW, Costa MM, Kandemir H, Vermaas M, Vu D, Zhao L, Arumugam E, Flakus A, Jurjević Ž, Kaliyaperumal M, Mahadevakumar S, Murugadoss R, Shivas RG, Tan YP, Wingfield MJ, Abell SE, Marney TS, Danteswari C, Darmostuk V, Denchev CM, Denchev TT, Etayo J, Gené J, Gunaseelan S, Hubka V, Illescas T, Jansen GM, Kezo K, Kumar S, Larsson E, Mufeeda KT, Pitek M, Rodriguez-Flakus P, Sarma PVSRN, Stryjak-Bogacka M, Torres-Garcia D, Vauras J, Acal DA, Akulov A, Alhudaib K, Asif M, Balashov S, Baral H-O, Baturo-Cieniewska A, Begerow D, Beja-Pereira A, Bianchinotti MV, Bilaski P, Chandranayaka S, Chellappan N, Cowan DA, Custódio FA, Czachura P, Delgado G, Desilva NI, Dijksterhuis J, Dueñas M, Eisvand P, Fachada V, Fournier J, Fritsche Y, Fuljer F, Ganga KGG, Guerra MP, Hansen K, Hywel-Jones N, Ismail AM, Jacobs CR, Jankowiak R, Karich A, Kemler M, Kisło K, Klofac W, Krisai-Greilhuber I, Latha KPD, Lebeuf R, Lopes ME, Lumyong S, Maciá-Vicente JG, Maggs-Kölling G, Magistà D, Manimohan P, Martín MP, Mazur E, Mehrabi-Koushki M, Miller AN, Mombert A, Ossowska EA, Patejuk K, Pereira OL, Piskorski S, Plaza M, Podile AR, Polhorský A, Pusz W, Raza M, Ruszkiewicz-Michalska M, Saba M, Sánchez RM, Singh R, Liwa L, Smith ME, Stefenon VM, Strašiftáková D, Suwannarach N, Szczepaska K, Telleria MT, Tennakoon DS, Thines M, Thorn RG, Urbaniak J, Vandervegte M, Vasan V, Vila-Viçosa C, Voglmayr H, Wrzosek M, Zappelini J, Groenewald JZ (2023) Fungal Planet description sheets: 1550–1613. Persoonia - Molecular Phylogeny and Evolution of Fungi 51: 280–417. https://doi.org/10.3767/persoonia.2023.51.08

da Silva NM, Reis GF, de Fátima Costa F, Grisolia ME, Geraldo MR, Lustosa BP, de Souza Lima BJ, Weiss VA, de Souza EM, Li R, Song Y (2023) Genome sequencing of *Cladophialophora exuberans*, a novel candidate for bioremediation of hydrocarbon and heavy metal polluted habitats. Fungal Biology 127: 1032–1042. https://doi.org/10.1016/j.funbio.2023.03.003

Dathong W (2016) Epiphytic lichen diversity in different areas of Nakhon Ratchasima, Thailand. Warasan Technology Suranaree 23: 135–140.

de Azevedo CMPS, Gomes RR, Vicente VA, Santos DWCL, Marques SG, do Nascimento MMF, Andrade CEW, Silva RR, Queiroz-Telles F, de Hoog GS (2015) *Fonsecaea pugnacius*, a novel agent of disseminated chromoblastomycosis. Journal of Clinical Microbiology 53: 2674–2685. https://doi.org/10.1128/JCM.00637-15

de Hoog GS, Weenink XO, van den Ende AH (1999) Taxonomy of the *Phialophora verrucosa* complex with the description of two new species. Studies in Mycology 1: 107–121.

de Hoog GS, Vicente VA, Najafzadeh MJ, Harrak MJ, Badali H, Seyedmousavi S (2011) Waterborne *Exophiala* species causing disease in cold-blooded animals. Persoonia 27: 46–72. https://doi.org/10.3767/003158511X614258

de León LR, Moreno-Perlín T, Castillo-Marenco T, Del Rayo Sánchez-Carbente M, Gostinčar C, Ramírez-Durán N, Ocaña AMF, Sánchez NC, Dávila-Ramos S, Gunde-Cimerman N, Batista-García RA (2025) Polyextremotolerant, opportunistic, and melanin-driven resilient black yeast *Exophiala dermatitidis* in environmental and clinical contexts. Scientific Reports 15: e6472. https://doi.org/10.1038/s41598-025-88595-z

de Souza Lima BJ, Voidaleski MF, Gomes RR, Fornari G, Soares JMB, Bombassaro A, Schneider GX, da Silva Soley B, de Azevedo CMPS, Menezes C, Moreno LF, Attili-Angelis D, Klisiowicz DR, de Hoog S, Vicente VA (2020) Selective isolation of agents of chromoblastomycosis from insect-associated environmental sources. Fungal Biology 124: 194–204. https://doi.org/10.1016/j.funbio.2020.02.002

Diederich P, Lawrey JD, Ertz D (2018) The 2018 classification and checklist of lichenicolous fungi, with 2000 non-lichenized, obligately lichenicolous taxa. The Bryologist 121: 340–425. https://doi.org/10.1639/0007-2745-121.3.340

Diederich P, Millanes AM, Wedin M, Lawrey JD (2022) Flora of Lichenicolous Fungi, Vol. 1, Basidiomycota. National Museum of Natural History, Luxembourg, 351 pp.

Diederich P, Ertz D, Braun U (2024) Flora of Lichenicolous Fungi, Vol. 2, Hyphomycetes. National Museum of Natural History, Luxembourg, 544 pp.

Dingley JM (1972) Some foliicolous Ascomycetes on ferns in Australia and New Zealand. The Genera *Rhagadolobium* P. Henn. & Lind. and *Lauterobachiella* Theiss. & Syd. New Zealand Journal of Botany 10: 74–86. https://doi.org/10.1080/0028825X.1972.10430213

Dong W, Hyde KD, Jayarama Bhat D, Zhang H (2018) Introducing *Aculeata aquatica* gen. et sp. nov., *Minimelanolocus thailandensis* sp. nov. and *Thysanorea aquatica* sp. nov. (Herpotrichiellaceae, Chaetothyriales) from freshwater in northern Thailand. Mycological Progress 17: 617–629. https://doi.org/10.1007/s11557-018-1389-2

Elkhateeb W, Daba G (2021) Fungi over fungi, endophytic fungi associated with mushroom fruiting bodies and lichens. Journal of Pharmacy and Pharmacology Research 4: 1–4. https://doi.org/10.31579/2693-7247/028

Ellis MB (1976) More dematiaceous Hyphomycetes. Commonwealth Mycological Institute, Kew, Surrey, England, 1–507. https://doi.org/10.1079/9780851983653.0000

Etayo J (2002) Lichenicolous fungi from Ecuador. II. Two new species on *Placopsis*. Anales del Jardin Botanico de Madrid 60: 19–25. https://doi.org/10.3989/ajbm.2002.v60.i1.72

Fernández-Mendoza F, Fleischhacker A, Kopun T, Grube M, Muggia L (2017) ITS1 metabarcoding highlights low specificity of lichen mycobiomes at a local scale. Molecular Ecology 26: 4811–4830. https://doi.org/10.1111/mec.14244

Gams W (2000) *Phialophora* and some similar morphologically little-differentiated anamorphs of divergent ascomycetes. Studies in Mycology 45: 187–199.

Gao H, Zou J, Li J, Zhao H (2016) Endolichenic fungi: A potential treasure trove for discovery of special structures and bioactive compounds. Studies in Natural Products Chemistry 48: 347–397. https://doi.org/10.1016/B978-0-444-63602-7.00011-4

Glass NL, Donaldson GC (1995) Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. Applied and Environmental Microbiology 61: 1323–1330. https://doi.org/10.1128/aem.61.4.1323-1330.1995

Hall TA (1999) BioEdit: A user–friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Hawksworth DL, Grube M (2020) Lichens redefined as complex ecosystems. The New Phytologist 227: 1281–1283. https://doi.org/10.1111/nph.16630

Heredia G, Arias RM, Castañeda-Ruiz RF, Minter DW (2014) New species of *Lobatopedis* and *Minimelanolocus* (anamorphic fungi) from a Mexican cloud forest. Nova Hedwigia 98: 31–40. https://doi.org/10.1127/0029-5035/2013/0146

Hernández-Restrepo M, Castañeda-Ruiz RF, Gené J, Guarro J, Minter DW, Stadler M (2013) Microfungi from Portugal: *Minimelanolocus manifestus* sp. nov. and *Vermiculariopsiella pediculata* comb. nov. Mycotaxon 122: 135–143. https://doi.org/10.5248/122.135

Hernández-Restrepo M, Giraldo A, Van Doorn R, Wingfield MJ, Groenewald JZ, Barreto RW, Colmán AA, Mansur PSC, Crous PW (2020) The genera of fungi–G6: *Arthrographis*, *Kramasamuha*, *Melnikomyces*, *Thysanorea*, and *Verruconis*. Fungal Systematics and Evolution 6: 1–24. https://doi.org/10.3114/fuse.2020.06.01

Hollinger JP, Lendemer JC (2021) *Capronia harrisiana* (Ascomycota, Chaetothyriales), a new lichenicolous species on *Crocodia aurata* from the southern Appalachian Mountains of southeastern North America. The Bryologist 124: 522–532. https://doi.org/10.1639/0007-2745-124.4.522

Hyde KD, Norphanphoun C, Chen J, Dissanayake AJ, Doilom M, Hongsanan S, Jayawardena RS, Jeewon R, Perera RH, Thongbai B, Wanasinghe DN, Wisitrassameewong K, Tibpromma S, Stadler M (2018) Thailand's amazing diversity: Up to 96% of fungi in northern Thailand may be novel. Fungal Diversity 93: 215–239. https://doi.org/10.1007/s13225-018-0415-7

Ide-Pérez MR, Sa'nchez-Reyes A, FolchMallol JL, Sa'nchez-Carbente MdR (2024) *Exophiala chapopotensis* sp. nov., an extremotolerant black yeast from an oil-polluted soil in Mexico; phylophenetic approach to species hypothesis in the Herpotrichiellaceae family. PLoS ONE 19: e0297232. https://doi.org/10.1371/journal.pone.0297232

Index Fungorum (2025) Index Fungorum. https://www.indexfungorum.org/ [Accessed 28 February 2025]

Jayawardena RS, Hyde KD, Chen YJ, Papp V, Palla B, Papp D, Bhunjun CS, Hurdeal VG, Senwanna C, Manawasinghe IS, Harischandra DL, Gautam AK, Avasthi S, Chuankid B, Goonasekara ID, Hongsanan S, Zeng XY, Liyanage KK, Liu NG, Karunarathna A, Hapuarachchi KK, Luangharn T, Raspé O, Brahmanage R, Doilom M, Lee HB, Mei L, Jeewon R, Huanraluek N, Chaiwan N, Stadler M, Wang Y (2020) One stop shop IV: taxonomic update with molecular phylogeny for important phytopathogenic genera: 76–100. Fungal Diversity 103: 87–218. https://doi.org/10.1007/s13225-020-00460-8

Jiang YL, Wu YM, Yang B, Xu JJ, Zhang ZG, Kong JH, Zhang TY (2017) *Cladosporium*, *Phialophora*, *Pseudoramichloridium* & *Ticogloea* spp. nov. from China. Mycotaxon 132: 677–684. https://doi.org/10.5248/132.677

Johnston P, Seifert KA, Stone J, Rossman AY, Marvanová L (2014) Recommendations on generic names competing for use in Leotiomycetes (Ascomycota). IMA Fungus 5: 91–120. https://doi.org/10.5598/imafungus.2014.05.01.11

Kaewsangsai S, Panyadee P, Panya A, Pandith H, Wangpakapattanawong P, Balslev H, Inta A (2024) Diversity of plant colorant species in a biodiversity hotspot in northern Thailand. Diversity 16: e194. https://doi.org/10.3390/d16040194

Kamal KP (1980) Fungi of Gorakhpur - XIII. Indian Phytopathology 33: 265–269.

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20: 1160–1166. https://doi.org/10.1093/bib/bbx108

Kellogg JJ, Raja HA (2017) Endolichenic fungi: A new source of rich bioactive secondary metabolites on the horizon. Phytochemistry Reviews 16: 271–293. https://doi.org/10.1007/s11101-016-9473-1

Kharwar RN, Singh RK (2004) Additions to the hyphomycete genus *Veronaea* as phytoparasitic species. Microbiological Research 159: 103–111. https://doi.org/10.1016/j.micres.2004.01.012

Krongdang S, Phokasem P, Venkatachalam K, Charoenphun N (2023) Edible insects in Thailand: An overview of status, properties, processing, and utilization in the food industry. Foods 12: e2162. https://doi.org/10.3390/foods12112162

Lawrey JD, Diederich P (2003) Lichenicolous fungi: Interactions, evolution, and biodiversity. The Bryologist 106: 80–120. https://doi.org/10.1639/0007-2745(2003)106[0080:LFIEAB]2.0.CO;2

Li JY, Qiao M, Peng J, Qian WY, Yang GZ, Yu ZF (2014) *Uncispora hainanensis* sp. nov. isolated from decayed leaves. Mycotaxon 129: 473–476. https://doi.org/10.5248/129.473

Li Y, Xiao J, De Hoog GS, Wang X, Wan Z, Yu J, Liu W, Li R (2017) Biodiversity and human-pathogenicity of *Phialophora verrucosa* and relatives in Chaetothyriales. Persoonia 38: 1–19. https://doi.org/10.3767/003158517X692779

Li J, Jeewon R, Phookamsak R, Bhat DJ, Mapook A, Chukeatirote E, Hyde KD, Lumyong S, Mckenzie EH (2018) *Marinophialophora garethjonesii* gen. et sp. nov.: A new hyphomycete associated with *Halocyphina* from marine habitats in Thailand. Phytotaxa 345: 1–12. https://doi.org/10.11646/phytotaxa.345.1.1

Liu YL, Xi PG, He XL, Jiang ZD (2013) *Phialophora avicenniae* sp. nov., a new endophytic fungus in *Avicennia marina* in China. Mycotaxon 124: 31–37. https://doi.org/10.5248/124.31

Liu LN, Razaq A, Atri NS, Bau T, Belbahri L, Chenari Bouket A, Chen LP, Deng C, Ilyas S, Khalid AN, Kitaura MJ, Kobayashi T, Li Y, Pedroso Lorenz A, Ma YH, Malysheva E, Malysheva V, Nuytinck J, Qiao M, Saini MK, Scur MC, Sharma S, Shu LL, Spirin V, Tanaka Y, Tojo M, Uzuhashi S, Valério-Júnior C, Verbeken A, Verma B, Wu RH, Xu JP, Yu ZF, Zeng H, Zhang B, Banerjee A, Beddiar A, Bordallo JJ, Dafri A, Dima B, Krisai-Greilhuber I, Lorenzini M, Mandal R, Morte A, Sarathi Nath P, Papp V, Pavlík J, Rodríguez A, Ševčíková H, Urban A, Voglmayr H, Zapparoli G (2018) Fungal Systematics and Evolution: FUSE 4. Sydowia 70: 211–286. https://doi.org/10.12905/0380.sydowia70-2018-0211

Lücking R, Hodkinson BP, Leavitt SD (2017) The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota—Approaching one thousand genera. The Bryologist 119: 361–416. https://doi.org/10.1639/0007-2745-119.4.361

Ma J, Zhang YD, Ma LG, Zhang XG (2011) Two new *Minimelanolocus* species from southern China. Mycotaxon 117: 131–135. https://doi.org/10.5248/117.131

Ma YR, Xia JW, Gao JM, Li XY, Castañeda Ruíz RF, Zhang XG, Li Z (2015) *Atrokylindriopsis*, a new genus of hyphomycetes from Hainan, China, with relationship to Chaetothyriales. Mycological Progress 14: e77. https://doi.org/10.1007/s11557-015-1071-x

Maduranga K, Attanayake RN, Santhirasegaram S, Weerakoon G, Paranagama PA (2018) Molecular phylogeny and bioprospecting of Endolichenic Fungi (ELF) inhabiting in the lichens collected from a mangrove ecosystem in Sri Lanka. PLoS ONE 13: e0200711. https://doi.org/10.1371/ journal.pone.0200711

Maneechan W, Prommi TO (2015) Diversity and distribution of aquatic insects in streams of the Mae Klong watershed, Western Thailand. Psyche (Cambridge, Massachusetts) 2015: e912451. https://doi.org/10.1155/2015/912451

Marincowitz S, Crous PW, Groenewald JZ, Wingfield MJ (2008) Microfungi Occurring on the Proteaceae in the Fynbos. (CBS biodiversity series; No. 7), CBS Fungal Biodiversity Centre, 166 pp.

Matsushima T (1989) Saprophytic microfungi from Taiwan. Part VI. Matsushima Mycological Memoirs 6: 1–68.

McGinnis MR, Schell WA, Carson J (1985) *Phaeoannellomyces* and the Phaeococcomycetaceae, new dematiaceous blastomycete taxa. Sabouraudia. Journal of Medical and Veterinary Mycology : Bi-Monthly Publication of the International Society for Human and Animal Mycology 23: 179–188. https://doi.org/10.1080/00362178585380281

Medlar EM (1915) A new fungus, *Phialophora verrucosa*, pathogenic for man. Mycologia 7: 200–203. https://doi.org/10.1080/00275514.1915.12021711

Miral A, Jargeat P, Mambu L, Rouaud I, Tranchimand S, Tomasi S (2022) Microbial community associated with the crustose lichen *Rhizocarpon geographicum* L. (DC.) living on oceanic seashore: A large source of diversity revealed by using multiple isolation methods. Environmental Microbiology Reports 14: 856–872. https://doi.org/10.1111/1758-2229.13105

Mitra S, Kambar S, Shanbhag SS (2024) *Pseudopithomyces Maydicus* and *Phialophora Chinensis* Rare Fungal Keratitis: Case Series, DNA Sequencing, Antifungal Susceptibility Patterns. Ocular Immunology and Inflammation 32: 2238–2242. https://doi.org/10.1080/09273948.2024. 2303352

Molnár K, Farkas E (2010) Current results on biological activities of lichen secondary metabolites: A review. Zeitschrift für Naturforschung C 65: 157–173. https://doi.org/10.1515/znc-2010-3-401

Moreno LF, Vicente VA, De Hoog S (2018) Black yeasts in the omics era: Achievements and challenges. Medical Mycology 56: S32–S41. https://doi.org/10.1093/mmy/myx129

Morgan-Jones G (1982) Notes on hyphomycetes. XL. new species of *Codinaea* and *Veronaea*. Mycotaxon 14: 175–180.

Moustafa AF, Abdul-Wahid OA (1990) *Veronaea constricta*, a new Hyphomycete from Egyptian soils. Mycotaxon 38: 167–171.

Muggia L, Grube M (2018) Fungal diversity in lichens: From extremotolerance to interaction with algae. Life (Chicago, Ill.) 8: e15. https://doi.org/10.3390/life8020015

Muggia L, Kopun T, Grube M (2017) Effects of growth media on the diversity of culturable fungi from lichens. Molecules 22: e824. https://doi.org/10.3390/molecules22050824

Müller K (2001) Pharmaceutically relevant metabolites from lichens. Applied Microbiology and Biotechnology 56: 9–16. https://doi.org/10.1007/s002530100684

Müller E, Petrini O, Fisher PJ, Samuels GJ, Rossman AY (1987) Taxonomy and anamorphs of the Herpotrichiellaceae with notes on generic synonymy. Transactions of the British Mycological Society 88: 63–74.

Munk A (1953) The system of the Pyrenomycetes. Dansk botanisk Arkiv 15(2): 1–163.

MycoBank (2025) MycoBank. https://www.mycobank.org [Accessed 25 March 2025]

Nepel M, Voglmayr H, Schönenberger J, Mayer VE (2014) High diversity and low specificity of chaetothyrialean fungi in carton galleries in a neotropical ant–plant association. PLoS ONE 9: e112756. https://doi.org/10.1371/journal.pone.0112756

Nimnoi P, Pirankham P, Srimuang K, Ruanpanun P (2024) Insights into soil nematode diversity and bacterial community of Thai jasmine rice rhizosphere from different paddy fields in Thailand. PeerJ 12: e17289. https://doi.org/10.7717/peerj.17289

Nylander J (2008) MrModeltest2 version 2.3 (programfor selectingDNA substitution models using PAUP*). Evolutionary Biology Centre, Uppsala, Sweden.

Oh SY, Yang JH, Woo JJ, Oh SO, Hur JS (2020) Diversity and distribution patterns of endolichenic fungi in Jeju Island, South Korea. Sustainability 12: e3769. https://doi.org/10.3390/su12093769

Pan HQ, Zhang TY (2009) Notes on soil dematiaceous hyphomycetes from the Yellow River source area, China. Mycosystema 28: 14–19. https://doi.org/10.1631/jzus.B0860002

Panta K (2020) lichens as bio-indicator for air pollution and their relevancy in Pokhara, Nepal. Himalayan Biodiversity 8: 47–51. https://doi.org/10.3126/hebids.v8i1.40241

Papendorf MC (1969) New South African soil fungi. Transactions of the British Mycological Society 52: 483–489.

Papendorf MC (1976) Notes on *Veronaea* including *V. compacta* sp. nov. Bothalia 12: 119–121.

Perera TWNK, Weerasinghe WRH, Attanayake RN, Paranagama PA (2022) Biodeterioration of low-density polyethylene by mangrove-associated endolichenic fungi and their enzymatic regimes. Letters in Applied Microbiology 75: 1526–1537. https://doi.org/10.1111/lam.13819

Phookamsak R, Hyde KD, Jeewon R, Bhat DJ, Jones EBG, Maharachchikumbura SSN, Raspé O, Karunarathna SC, Wanasinghe DN, Hongsanan S, Doilom M, Tennakoon DS, Machado AR, Firmino AL, Ghosh A, Karunarathna A, Mešić A, Dutta AK, Thongbai B, Devadatha B, Norphanphoun C, Senwanna C, Wei D, Pem D, Ackah FK, Wang GN, Jiang HB, Madrid H, Lee HB, Goonasekara ID, Manawasinghe IS, Kušan I, Josep Cano J, Gené J, Li JF, Das K, Acharya K, Raj KNA, Latha KPD, Chethana KWT, He MQ, Dueñas M, Jadan M, Martín MP, Samarakoon MC, Dayarathne MC, Raza M, Park MS, Telleria MT, Chaiwan N, Matočec N, de Silva NI, Pereira OL, Singh PN, Manimohan P, Uniyal P, Shang QJ, Bhatt RP, Perera RH, Alvarenga RLM, Nogal-Prata S, Singh SK, Vadthanarat S, Oh SY, Huang SK, Rana S, Konta S, Paloi S, Jayasiri SC, Jeon SJ, Mehmood T, Gibertoni TB, Nguyen TTT, Singh U, Thiyagaraja V, Sarma VV, Dong W, Yu XD, Lu YZ, Lim YW, Chen Y, Tkalčec Z, Zhang ZF, Luo ZL, Daranagama DA, Thambugala KM, Tibpromma S, Camporesi E, Bulgakov TS, Dissanayake AJ, Senanayake IC, Dai DQ, Tang LZ, Khan S, Zhang H, Promputtha I, Cai L, Chomnunti P, Zhao RL, Lumyong S, Boonmee S, Wen TC, Mortimer PE, Xu JC (2019) Fungal diversity notes 929–1035: Taxonomic and phylogenetic contributions on genera and species of fungi. Fungal Diversity 95: 1–273. https://doi.org/10.1007/s13225-019-00421-w

Ply B, Cañete-Gibas CF, Sanders C, Wiederhold NP, Dandar RA, Sheppard JD, Cheung AY (2023) *Phialophora chinensis* fungal keratitis: An initial case report and species identification. American Journal of Ophthalmology Case Reports 29: e101800. https://doi.org/10.1016/j.ajoc.2023.101800

Pruvot C, Messagier AL, Garcia-Hermoso D, Lebailly F, Aglae C, Desbois-Nogard N (2023) First case of subcutaneous cystic phaeohyphomycosis due to *Phialophora chinensis* in a kidney transplant recipient in Martinique. Medical Mycology Case Reports 39: 18–22. https://doi.org/10.1016/j.mmcr.2022.12.003

Quan Y, Muggia L, Moreno LF, Wang M, Al-Hatmi AM, da Silva Menezes N, Shi D, Deng S, Ahmed S, Hyde KD, Vicente VA (2020) A re-evaluation of the Chaetothyriales using criteria of comparative biology. Fungal Diversity 103: 47–85. https://doi.org/10.1007/s13225-020-00452-8

Quan Y, da Silva NM, de Souza Lima BJF, de Hoog S, Vicente VA, Mayer V, Kang Y, Shi D (2022) Black fungi and ants: A genomic comparison of species inhabiting carton nests versus domatia. IMA Fungus 13: e4. https://doi.org/10.1186/s43008-022-00091-5

Quan Y, Deng S, Prenafeta-Boldů FX, Mayer VE, Muggia L, Cometto A, Vicente VA, da Silva NM, Grisolia ME, Song Y, Ahmed SA, Niu X, de Souza Lima BJF, Feng P, Vitale RG, Teixeira M, Sudhadham M, de Azevedo CPeS, Bocca A, Haase G, Selbmann L, Shi D, Kang Y, de Hoog S (2024) The origin of human pathogenicity and biological interactions in Chaetothyriales. Fungal Diversity 125: 99–120. https://doi.org/10.1007/s13225-023-00518-3

Rambaut A (2016) FigTree, version 1.4.3. Institute of Evolutionary Biology, University of Edinburgh, UK. http://tree.bio.ed.ac.uk/software/figtree [Accessed 19 October 2024]

Rathnayaka AR, Tennakoon DS, Jones GE, Wanasinghe DN, Bhat DJ, Priyashantha AH, Stephenson SL, Tibpromma S, Karunarathna SC (2024) Significance of precise documentation of hosts and geospatial data of fungal collections, with an emphasis on plant-associated fungi. New Zealand Journal of Botany 63: 462–489. https://doi.org/10.1080/0028825X.2024.2381734

Réblová M, Gams W, Štěpánek V (2011) The new hyphomycete genera Brachyalara and Infundichalara, the similar Exochalara and species of '*Phialophora* sect. *Catenulatae*' (Leotiomycetes). Fungal Diversity 46: 67–86. https://doi.org/10.1007/s13225-010-0077-6

Réblová M, Untereiner WA, Réblová K (2013) Novel evolutionary lineages revealed in the Chaetothyriales (Fungi) based on multigene phylogenetic analyses and comparison of ITS secondary structure. PLoS ONE 8: e63547. https://doi.org/10.1371/journal.pone.0063547

Réblová M, Untereiner WA, Štěpánek V, Gams W (2017) Disentangling *Phialophora* section *Catenulatae*: Dispositionof taxa with pigmented conidiophores and recognition of a new subclass, Sclerococcomycetidae (Eurotiomycetes). Mycological Progress 16: 27–46. https://doi.org/10.1007/s11557-016-1248-y

Roeun V, Esther Das K, Lee SY, Jung HY (2022) Molecular and morphological characterization of two novel species from soil and beetles (*Dorcus titanus castanicolor*) in Korea. Mycobiology 50: 429–438. https://doi.org/10.1080/12298093.2022.2149927

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Roux C, Pinaul P, Ertz D, Gardiennet A (2020) Deux *Capronia* s. l. (Ascomycota, Chaetothyriales) lichénicoles sur *Cladonia*. Bulletin de la Société Linnéenne de Provence 71: 75–86.

Sánchez RM, Miller AN, Bianchinotti MV (2019) New species of *Capronia* (Herpotrichiellaceae, Ascomycota) from Patagonian forests, Argentina. Plant and Fungal Systematics. 64: 81–90. https://doi.org/10.2478/pfs-2019-0009

Sang H, Zheng XE, Kong QT, Zhou WQ, He W, Lv GX, Shen YN, Liu WD (2011) A rare complication of ear piercing: A case of subcutaneous phaeohyphomycosis caused by *Veronaea botryosa* in China. Medical Mycology 49: 296–302. https://doi.org/10.3109/13693786.2010.513340

Schol-Schwarz MB (1970) Revision of the genus *Phialophora* (Moniliales). Persoonia 6: 59–94.

Si H, Wang Y, Liu Y, Li S, Bose T, Chang R (2023) Fungal diversity associated with thirty-eight lichen species revealed a new genus of endolichenic fungi, *Intumescentia* gen. nov. (Teratosphaeriaceae). Journal of Fungi 9: e423. https://doi.org/10.3390/jof9040423

Sinclair RC, Morgan-Jones G (1979) Notes on hyphomycetes. XXVI. *Uncispora harroldii* gen. et sp. nov. Mycotaxon 8: 140–143.

Singh RP, Kamal K, Abbasi P (1981) A new species of *Veronaea*. Current Science 50: 236–238.

Singh BN, Upreti DK, Gupta VK, Dai XF, Jiang Y (2017) Endolichenic fungi: A hidden reservoir of next generation biopharmaceuticals. Trends in Biotechnology 35: 808–813. https://doi.org/10.1016/j.tibtech.2017.03.003

Soares DJ, Barreto RW (2008) Fungal pathogens of the invasive riparian weed *Hedychium coronarium* from Brazil and their potential for biological control. Fungal Diversity 28: 85–96. https://doi.org/10.1071/DN08034

Song Y, Menezes da Silva N, Vicente VA, Quan Y, Teixeira M, Gong J, de Hoog S, Li R (2021) Comparative genomics of opportunistic *Phialophora* species involved in divergent disease types. Mycoses 64: 555–568. https://doi.org/10.1111/myc.13244

Soto E, Richey C, Reichley SR, Stevens B, Kenelty KV, Lewis J, Byrne B, Wiederhold NP, Waltzek TB, Sheley MF, Camus A, Griffin MJ (2017) Diversity of *Veronaea botryosa* from different hosts and evaluation of laboratory challenge models for

phaeohyphomycosis in *Acipenser transmontanus*. Diseases of Aquatic Organisms 125: 7–18. https://doi.org/10.3354/dao03134

Sousa GS, De Oliveira RS, De Souza AB, Monteiro RC, Santo EP, Franco Filho LC, Da Silva SH (2024) Identification of chromoblastomycosis and phaeohyphomycosis agents through ITS-RFLP. Journal of Fungi 10: e159. https://doi.org/10.3390/jof10020159

Spegazzini C (1909) Mycetes Argentinenses. Series IV. Anales del Museo Nacional de Historia Natural Buenos Aires 19: 257–458.

Su P, Chen Y, Syed A, Bahkali AH, Maharachchikumbura SS (2023) Taxonomic novelty in Sichuan Province, China: *Veronaea polyconidia* sp. nov. (Herpotrichiellaceae), a new addition to hyphomycetous fungi. Phytotaxa 632: 118–130. https://doi.org/10.11646/phytotaxa.632.2.2

Suryanarayanan TS, Thirunavukkarasu N (2017) Endolichenic fungi: The lesser known fungal associates of lichens. Mycology 8: 189–196. https://doi.org/10.1080/21501203.2017.1352048

Suryanarayanan TS, Govindarajulu MB, Rajamani T, Tripathi M, Joshi Y (2017) Endolichenic fungi in lichens of Champawat district, Uttarakhand, northern India. Mycological Progress 16: 205–211. https://doi.org/10.1007/s11557-016-1268-7

Swofford DL (2002) PAUP*: phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland.

Tanasupawat S (2009) Thai lactic acid bacteria: Diversity and applications. Srinakharinwirot Science Journal 25: 1–3.

Tayung K (2022) Exploration of endophytic fungi for applications in agriculture and medicine. Journal of Mycopathological Research 60: 1–11.

Teixeira MM, Moreno LF, Stielow BJ, Muszewska A, Hainaut M, Gonzaga L, Abouelleil A, Patané JSL, Priest M, Souza R, Young S, Ferreira KS, Zeng Q, da Cunha MML, Gladki A, Barker B, Vicente VA, de Souza EM, Almeida S, Henrissat B, Vasconcelos ATR, Deng S, Voglmayr H, Moussa TAA, Gorbushina A, Felipe MSS, Cuomo CA, de Hoog GS (2017) Exploring the genomic diversity of black yeasts and relatives (Chaetothyriales, Ascomycota). Studies in Mycology 86: 1–28. https://doi.org/10.1016/j.simyco.2017.01.001

Thitla T, Kumla J, Khuna S, Lumyong S, Suwannarach N (2022) Species diversity, distribution, and phylogeny of Exophiala with the addition of four new species from Thailand. Journal of Fungi 8: e766. https://doi.org/10.3390/jof8080766

Thitla T, Kumla J, Hongsanan S, Senwanna C, Khuna S, Lumyong S, Suwannarach N (2023) Exploring diversity rock-inhabiting fungi from northern Thailand: A new genus and three new species belonged to the family Herpotrichiellaceae. Frontiers in Cellular and Infection Microbiology 13: e1252482. https://doi.org/10.3389/fcimb.2023.1252482

Thitla T, Kumla J, Khuna S, Srinuanpan S, Hongsanan S, Senwanna C, Tibpromma S, Pathom-aree W, Lumyong S, Suwannarach N (2024) Research advances in taxonomy, phylogeny, ecology, and distribution of the genus *Cladophialophora*. Chaing Mai Journal of Science 51: e2024004. https://doi.org/10.12982/CMJS.2024.004

Tian Q, Doilom M, Luo ZL, Chomnunti P, Bhat JD, Xu JC, Hyde KD (2016) Introducing *Melanoctona tectonae* gen. et sp. nov. and *Minimelanolocus yunnanensis* sp. nov. (Herpotrichiellaceae, Chaetothyriales). Cryptogamie, Mycologie 37: 477–492. https://doi.org/10.7872/crym/v37.iss 4.2016.477

Tian Q, Chomnunti P, Lumyong S, Liu JK, Hyde KD (2021) Phylogenetic relationships and morphological reappraisal of Chaetothyriales. Mycosphere 12: 1157–1261. https://doi.org/10.5943/mycosphere/12/1/15

Torres-Garcia D, García D, Réblová M, Jurjević Ž, Hubka V, Gené J (2023) Diversity and novel lineages of black yeasts in Chaetothyriales from freshwater sediments in Spain. Persoonia - Molecular Phylogeny and Evolution of Fungi 51: 194–228. https://doi.org/10.3767/persoonia.2023.51.05

Toure S, Millot M, Ory L, Roullier C, Khaldi Z, Pichon V, Girardot M, Imbert C, Mambu L (2022) Access to anti-biofilm compounds from endolichenic fungi using a bioguided networking screening. Journal of Fungi 8: e1012. https://doi.org/10.3390/jof8101012

Tsurykau A, Etayo J (2017) *Capronia suijae* (Herpotrichiellaceae, Eurotiomycetes), a new fungus on Xanthoria parietina from Belarus, with a key to the lichenicolous species growing on *Xanthoria* s. str. Lichenologist 49: 1–12. https://doi.org/10.1017/S0024282916000530

Tungmunnithum D, Drouet S, Lorenzo JM, Hano C (2022) Effect of traditional cooking and in vitro gastrointestinal digestion of the ten most consumed beans from the Fabaceae family in Thailand on their phytochemicals, anti-oxidant and anti-diabetic potentials. Plants 11: e67. https://doi.org/10.3390/plants11010067

U'Ren JM, Lutzoni F, Miadlikowska J, Laetsch AD, Arnold AE (2012) Host and geographic structure of endophytic and endolichenic fungi at a continental scale. American Journal of Botany 99: 898–914. https://doi.org/10.3732/ajb.1100459

U'Ren JM, Lutzoni F, Miadlikowska J, Arnold AE (2010) Community analysis reveals close affinities between endophytic and endolichenic fungi in mosses and lichens. Microbial Ecology 60: 340–353. https://doi.org/10.1007/s00248-010-9698-2

Untereiner WA (1997) Taxonomy of selected members of the ascomycete genus *Capronia* with notes on anamorph-teleomorph connections. Mycologia 89: 120–131. https://doi.org/10.1080/00275514.1997.12026763

Untereiner WA (2000) *Capronia* and its anamorphs: Exploring the value of morphological and molecular characters in the systematics of the Herpotrichiellaceae. Studies in Mycology 45: 141–148.

Untereiner WA, Naveau FA (1999) Molecular systematics of the Herpotrichiellaceae with an assessment of the phylogenetic positions of *Exophiala dermatitidis* and *Phialophora americana*. Mycologia 91: 67–83. https://doi.org/10.1080/00275514.1999.12060994

Untereiner WA, Straus NA, Malloch D (1995) A molecular-morphotaxonomic approach to the systematics of the Herpotrichiellaceae and allied black yeasts. Mycological Research 99: 897–913. https://doi.org/10.1016/S0953-7562(09)80748-X

Untereiner WA, Angus A, Réblová M, Orr MJ (2008) Systematics of the *Phialophora verrucosa* complex: New insights from analyses of β- tubulin, large subunit nuclear rDNA and ITS sequences. Botany 86: 742–750. https://doi.org/10.1139/B08-057

Untereiner WA, Gueidan C, Orr MJ, Diederich P (2011) The phylogenetic position of the lichenicolous ascomycete *Capronia peltigerae*. Fungal Diversity 49: 225–233. https://doi.org/10.1007/s13225-011-0097-x

Untereiner WA, Yue Q, Chen L, Li Y, Bills GF, Štěpánek V, Reblova M (2019) *Phialophora* section *Catenulatae* disassembled: New genera, species, and combinations and a new family encompassing taxa with cleistothecial ascomata and phialidic asexual states. Mycologia 111: 998–1027. https://doi.org/10.1080/00275514.2019.1663106

Varlı M, Pham HT, Kim SM, Taş İ, Gamage CD, Zhou R, Pulat S, Park SY, Sesal NC, Hur JS, Kang KB (2022) An acetonic extract and secondary metabolites from the endolichenic fungus *Nemania* sp. EL006872 exhibit immune checkpoint inhibitory activity in lung cancer cell. Frontiers in Pharmacology 13: e986946. https://doi.org/10.3389/fphar.2022.986946

Varlı M, Ngo MT, Kim SM, Taş İ, Zhou R, Gamage CDB, Pulat S, Park SY, Sesal NC, Hur JS, Kang KB, Kim H (2023) A fatty acid-rich fraction of an endolichenic fungus *Pho-*

ma sp. suppresses immune checkpoint markers via AhR/ARNT and ESR1. Heliyon 9: e19185. https://doi.org/10.1016/j.heliyon.2023.e19185

Vicente VA, Orélis-Ribeiro R, Najafzadeh MJ, Sun J, Schier Guerra R, Miesch S, Ostrensky A, Meis JF, Klaassen CH, de Hoog GS, Boeger WA (2012) Black yeast-like fungi associated with Lethargic Crab Disease (LCD) in the mangrove-land crab, *Ucides cordatus* (Ocypodidae). Veterinary Microbiology 158: 109–122. https://doi.org/10.1016/j.vetmic.2012.01.031

Vicente V, Najafzadeh M, Sun J, Gomes R, Robl D, Marques S, Azevedo C, De Hoog G (2014) Environmental siblings of black agents of human chromoblastomycosis. Fungal Diversity 65: 47–63. https://doi.org/10.1007/s13225-013-0246-5

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172: 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Wang Y, Zheng Y, Wang X, Wei X, Wei J (2016) Lichen-associated fungal community in *Hypogymnia hypotrypa* (Parmeliaceae, Ascomycota) affected by geographic distribution and altitude. Frontiers in Microbiology 7: 1231. https://doi.org/10.3389/fmicb.2016.01231

Wethalawe AN, Alwis YV, Udukala DN, Paranagama PA (2021) Antimicrobial compounds isolated from endolichenic fungi: A review. Molecules 26: e3901. https://doi.org/10.3390/molecules26133901

White TJ, Bruns T, Lee SJWT, Taylor JL (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR Protocols: A Guide to Methods and Applications. Academic Press, San Diego, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wijayawardene NN, Hyde KD, Al-Ani LKT, Tedersoo L, Haelewaters D, Rajeshkumar KC, Zhao RL, Aptroot A, Leontyev DV, Saxena RK, Tokarev YS, Dai DQ, Letcher PM, Stephenson SL, Ertz D, Lumbsch HT, Kukwa M, Issi IV, Madrid H, Phillips AJL, Selbmann L, Pfliegler WP, Horváth E, Bensch K, Kirk PM, Kolaříková K, Raja HA, Radek R, Papp V, Dima B, Ma J, Malosso E, Takamatsu S, Rambold G, Gannibal PB, Triebel D, Gautam AK, Avasthi S, Suetrong S, Timdal E, Fryar SC, Delgado G, Réblová M, Doilom M, Dolatabadi S, Pawłowska J, Humber RA, Kodsueb R, Sánchez-Castro I, Goto BT, Silva DKA, de Souza FA, Oehl F, da Silva GA, Silva IR, Błaszkowski J, Jobim K, Maia LC, Barbosa FR, Fiuza PO, Divakar PK, Shenoy BD, Castañeda-Ruiz RF, Somrithipol S, Lateef AA, Karunarathna SC, Tibpromma S, Mortimer PE, Wanasinghe DN, Phookamsak R, Xu J, Wang Y, Tian F, Alvarado P, Li DW, Kušan I, Matočec N, Maharachchikumbura SSN, Papizadeh M, Heredia G, Wartchow F, Bakhshi M, Boehm E, Youssef N, Hustad VP, Lawrey JD, Santiago ALCMA, Bezerra JDP, Souza-Motta CM, Firmino AL, Tian Q, Houbraken J, Hongsanan S, Tanaka K, Dissanayake AJ, Monteiro JS, Grossart HP, Suija A, Weerakoon G, Etayo J, Tsurykau A, Vázquez V, Mungai P, Damm U, Li QR, Zhang H, Boonmee S, Lu YZ, Becerra AG, Kendrick B, Brearley FQ, Motiejūnaitė J, Sharma B, Khare R, Gaikwad S, Wijesundara DSA, Tang LZ, He MQ, Flakus A, Rodriguez-Flakus P, Zhurbenko MP, McKenzie EHC, Stadler M, Bhat DJ, Liu JK, Raza M, Jeewon R, Nassonova ES, Prieto M, Jayalal RGU, Erdoğdu M, Yurkov A, Schnittler M, Shchepin ON, Novozhilov YK, Silva-Filho AGS, Liu P, Cavender JC, Kang Y, Mohammad S, Zhang LF, Xu RF, Li YM, Dayarathne MC, Ekanayaka AH, Wen TC, Deng CY, Pereira OL, Navathe S, Hawksworth DL, Fan XL, Dissanayake LS, Kuhnert E, Grossart HP, Thines M (2020) Outline of Fungi and fungus-like taxa. Mycosphere 11: 1060–1456. https://doi.org/10.5943/mycosphere/11/1/8

Wijayawardene NN, Hyde KD, Dai DQ, Sánchez-García M, Goto BT, Saxena RK, Erdoğdu M, Selçuk F, Rajeshkumar KC, Aptroot A, Błaszkowski J, Boonyuen N, da Silva GA,

de Souza FA, Dong W, Ertz D, Haelewaters D, Jones EBG, Karunarathna SC, Kirk PM, Kukwa M, Kumla J, Leontyev DV, Lumbsch HT, Maharachchikumbura SSN, Marguno F, Martínez-Rodríguez P, Mešić A, Monteiro JS, Oehl F, Pawłowska J, Pem D, Pfliegler WP, Phillips AJL, Pošta A, He MQ, Li JX, Raza M, Sruthi OP, Suetrong S, Suwannarach N, Tedersoo L, Thiyagaraja V, Tibpromma S, Tkalčec Z, Tokarev YS, Wanasinghe DN, Wijesundara DSA, Wimalaseana SDMK, Madrid H, Zhang GQ, Gao Y, Sánchez-Castro I, Tang LZ, Stadler M, Yurkov A, Thines M (2022) Outline of Fungi and fungus-like taxa—2021. Mycosphere 13: 53–453. https://doi.org/10.5943/mycosphere/13/1/2

Yan ZH, Rogers SO, Wang CJ (1995) Assessment of *Phialophora* species based on ribosomal DNA internal transcribed spacers and morphology. Mycologia 87: 72–83. https://doi.org/10.1080/00275514.1995.12026505

Yang JH, Oh SY, Kim W, Woo JJ, Kim H, Hur JS (2021) Effect of isolation conditions on diversity of endolichenic fungal communities from a foliose lichen, *Parmotrema tinctorum*. Journal of Fungi 7: e335. https://doi.org/10.3390/jof7050335

Yang JH, Oh SY, Kim W, Hur JS (2022) Endolichenic fungal community analysis by pure culture isolation and metabarcoding: A case study of *Parmotrema tinctorum*. Mycobiology 50: 55–65. https://doi.org/10.1080/12298093.2022.2040112

Yang J, Liu LL, Jones EG, Hyde KD, Liu ZY, Bao DF, Liu NG, Li WL, Shen HW, Yu XD, Liu JK (2023) Freshwater fungi from karst landscapes in China and Thailand. Fungal Diversity 119: 1–212. https://doi.org/10.1007/s13225-023-0051

Zhan F, He Y, Zu Y, Li T, Zhao Z (2011) Characterization of melanin isolated from a dark septate endophyte (DSE), *Exophiala pisciphila*. World Journal of Microbiology & Biotechnology 27: 2483–2489. https://doi.org/10.1007/s11274-011-0712-8

Zhang K, Fu HB, Zhang XG (2009) Taxonomic studies of *Minimelanolocus* from Yunnan, China. Mycotaxon 109: 95–101. https://doi.org/10.5248/109.95

Zhang T, Wei XL, Wei YZ, Liu HY, Yu LY (2016) Diversity and distribution of cultured endolichenic fungi in the Ny-Ålesund region, svalbard (high arctic). Extremophiles 20: 461–470. https://doi.org/10.1007/s00792-016-0836-8

Zhang D, Gu G, Zhang B, Wang Y, Bai J, Fang Y, Zhang T, Dai S, Cen S, Yu L (2021) New phenol and chromone derivatives from the endolichenic fungus *Daldinia* species and their antiviral activities. RSC Advances 11: 22489–22494. https://doi.org/10.1039/D1RA03754D

Zhang W, Ran Q, Li H, Lou H (2024) Endolichenic fungi: A promising medicinal microbial resource to discover bioactive natural molecules—an update. Journal of Fungi 10: e99. https://doi.org/10.3390/jof10020099

Zhao Y, Wang M, Xu B (2021) A comprehensive review on secondary metabolites and health-promoting effects of edible lichen. Journal of Functional Foods 80: e104283. https://doi.org/10.1016/j.jff.2020.10428